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FECUNDITY OF THE PACIFIC HAKE, *MERLUCCIUS PRODUCTUS* (AYRES)[1]

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Measurements of yolked eggs in the developing ovaries of female hake formed bimodal distributions. The numbers of advanced yolked eggs increased with both length and weight of the fish. The smallest of 22 hake, 346 mm long contained 80,000 eggs, while the longest, 688 mm, contained 496,000 eggs: The number of eggs may be estimated by multiplying fish length cubed by 0.00142, or by multiplying weight by 192. Weights ranged from 300 to 2,750 g, and these fish contained 46,000 and 496,000 eggs respectively. There was considerable variation in numbers of advanced eggs produced regardless of size. A fish 395 mm long that weighed 500 g contained 298,000 eggs, while a larger specimen, 433 mm and 600 g, contained only 64,000 eggs. Although two sizes of yolked eggs were present in the ovaries, the peculiarities of the distribution and the relatively short spawning season indicate that the hake spawns only once a year.

INTRODUCTION

During the 15 years of the California Cooperative Oceanic Fisheries Investigations' surveys of the California Current area, Pacific hake have ranked second in abundance among larvae taken in plankton tows. Hake have accounted for about 19 percent of the total larvae taken; northern anchovy (*Engraulis mordax* Girard) larvae, the most abundant, have accounted for about 34 percent. To estimate the biomass of the parent stock of a fish species from the occurrence of eggs or larvae in the plankton, one must know the average number of times each female spawns in a year and the number of eggs produced at each spawning.

METHODS

My estimates of hake fecundity are based on 22 females with well-developed ovaries taken in March 1963 off northern Baja California. Standard length was recorded to the nearest millimeter and weight to the nearest 50 grams. The specimens were 346 to 688 mm long and weighed from 300 to 2,750 g (Table 1). Ovary weight ranged from 13.1 g in one of the small specimens to 196.8 g in the largest; both of these ovaries were at about the same developmental stage.

Frequency distributions of the diameters of eggs containing yolk were determined from ovarian samples. Each ovary contained a distinct group of large, yolked eggs plus a more or less distinct group, or groups, of small, yolked eggs. Ratios of numbers of larger eggs to smaller ones were determined from the frequency distributions.

The ovarian samples used to estimate egg numbers were larger than those used to obtain frequency distributions. The samples were weighed,

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[1] Submitted for publication October 1965.

and only the eggs in the most advanced stage of development were counted under a binocular microscope. Egg counts varied widely among different specimens without relation to ovary weight and egg size, so more than one count was made on ovaries showing high deviations from the number expected. Every additional count agreed with the first count for the same fish. These variations in egg counts appeared to be caused by differences in the amount of tissue other than yolked eggs, and by variations in size and numbers of the smaller, yolked eggs.

Of the 22 fish examined, 15 contained opaque, advanced eggs with mean diameters of 0.66 to 0.80 mm, and 7 contained translucent, advanced eggs with mean diameters of 0.84 to 1.12 mm; both of these groups of eggs formed distinct modes when frequencies were plotted. The translucent eggs were more distorted by preservative than the opaque eggs and therefore more difficult to measure. Ahlstrom and Counts (1955) reported that hake eggs taken in plankton tows had diameters of 1.07 to 1.18 mm. None of the ovaries containing translucent eggs appeared to be partly spent.

LENGTH AND FECUNDITY

There is an obvious relation between the number of eggs in an advanced stage of development and fish length, although there is considerable spread of values about the line fitted to the data (Figure 1). The greatest deviation is exhibited by a 395 mm hake that contained 278,000 advanced eggs, and one approximately the same size (391 mm) that contained only 71,500 eggs, or about one-quarter as many. Since the ovaries of the 395 mm hake weighed 3½ times as much as those of

TABLE 1

Fecundity Data for 22 Hake from Northern Baja California, March 1963

Standard length (mm)	Weight (grams)	Gonad weight (grams)	Advanced eggs		Eggs per gram of fish
			Number (thousands)	Diameter (mm)	
688	2,750	196.8	496	.60– .76	180
577	1,600	106.7	147	.56– .74	92
552	1,350	68.3	163	.58– .76	120
533	1,100	52.9	120	.60– .76	115
515	950	57.4	96	.80–1.00*	101
503	950	74.2	242	.64– .88	256
497	900	88.2	292	.68– .84	324
481	850	64.7	188	.70– .90	221
475	750	83.6	252	.70– .90	336
447	650	87.4	108	1.00–1.22*	166
442	600	43.8	137	.56– .74	228
433	600	42.9	64	.80–1.04*	107
431	600	49.9	93	.80–1.00*	155
422	550	41.2	122	.60– .80	221
395	500	82.0	278	.58– .76	556
391	400	24.8	72	.60– .80	179
384	350	18.5	43	.58– .78	122
373	400	13.1	38	.62– .80	96
367	400	13.7	33	.66– .82	83
358	450	51.4	113	.88–1.06*	251
351	300	30.0	46	.82–1.04*	153
346	500	45.4	80	.76– .92*	160

* Translucent eggs.

the 391 mm hake, and the advanced eggs of the 395 mm hake were smaller (mean diameter 0.68 mm) than those of the 391 mm fish (mean diameter 0.72 mm), the differences appear to be real.

WEIGHT AND FECUNDITY

The number of advanced eggs ranged from 33,000 in a 400 g hake to 496,000 in a 2,750 g hake. Advanced eggs per gram of female hake ranged from 83 to 556 and averaged 192. The relative fecundity (eggs per gram of fish) may be lower in large and small hake than in fish

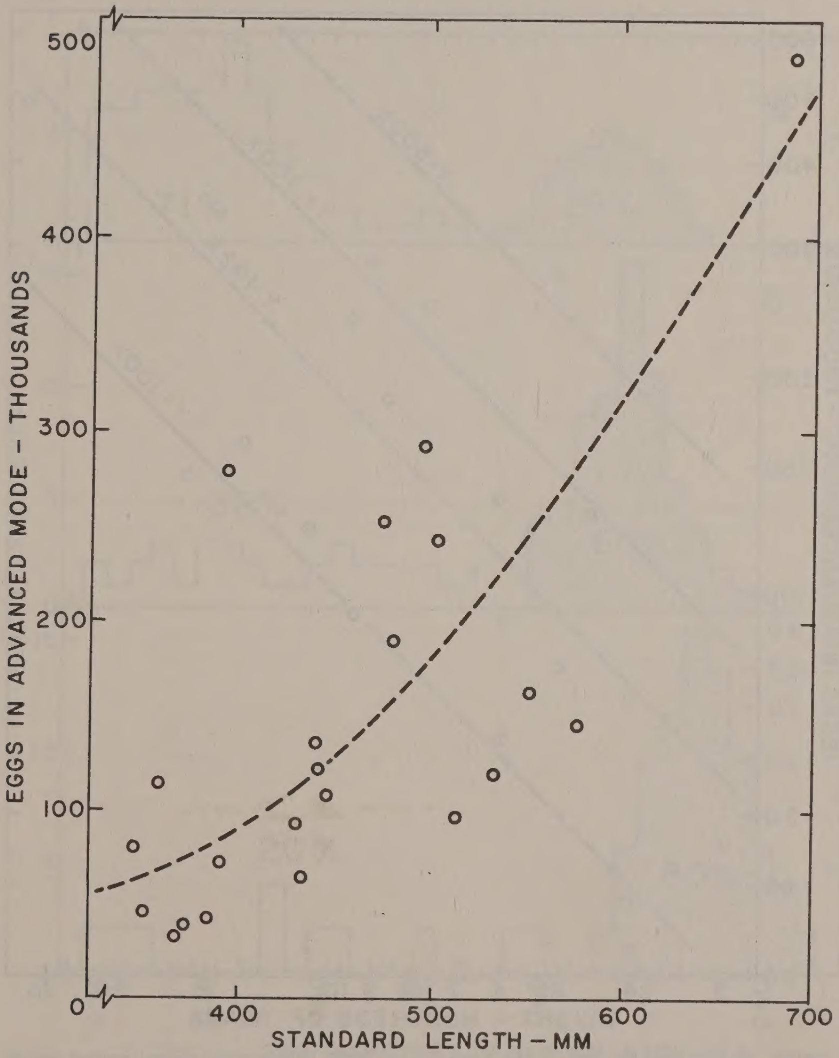

FIGURE 1. Estimates of numbers of advanced eggs in 22 hake ovaries plotted against standard length of female hake. The line describing the data is $Y_c = 0.00142X^3$ in which Y_c = the calculated numbers of eggs and X^3 = length of fish cubed.

of intermediate size (Figure 2). Eggs per gram of fish averaged 127 (range 83–179) for the 5 fish weighing 300–400 g, 127 (range 92–180) for the 4 fish weighing 1,100–2,750 g, and 237 (range 101–556) for the 13 fish weighing 450–950 g.

NUMBER OF SPAWNINGS

Ahlstrom and Counts (1955) found, from extensive plankton sampling off the coasts of California and Baja California in 1951 and 1952, that 50 to 60 percent of the hake larvae were taken in March, and 98

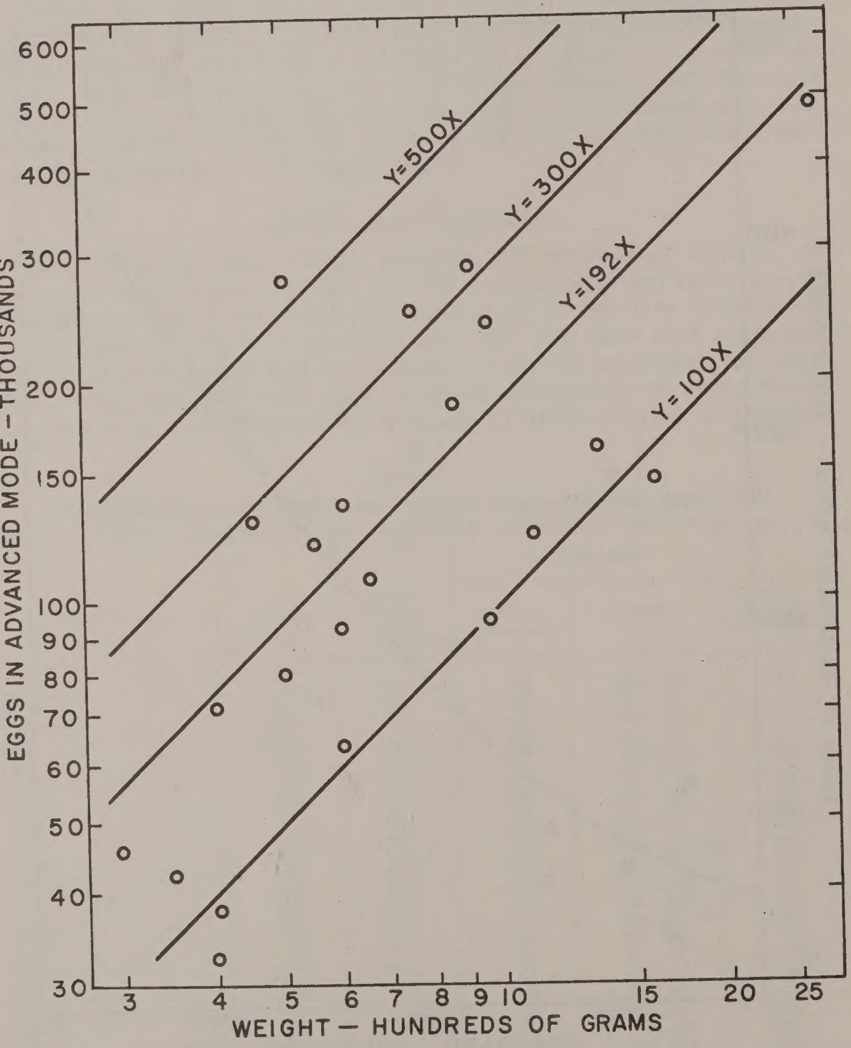

FIGURE 2. Estimates of numbers of advanced eggs in 22 hake ovaries plotted against weight of female hake. The lines represent 100 eggs per gram of fish, 192 (the average describing the sample), 300, and 500 eggs per gram of fish respectively.

percent in February, March, and April. Such a restricted spawning period would indicate that only one spawning occurred each year.

On the other hand, the presence of more than one size group of yolked eggs in the ovary has been interpreted by many investigators to indicate that more than one spawning may occur per year. The ratios of numbers of advanced eggs to smaller eggs varied considerably among the 22 hake examined. The ratios of large to small eggs for three hake were approximately 1:2.5, 1:0.5 and 1:0.25 (Figures 3A, 3B, 3C). The 1:2.5 ratio (Figure 3A) represents a hake with a very low relative fecundity, 92 advanced eggs per gram of fish, while the 1:0.5 ratio (Figure 3B)

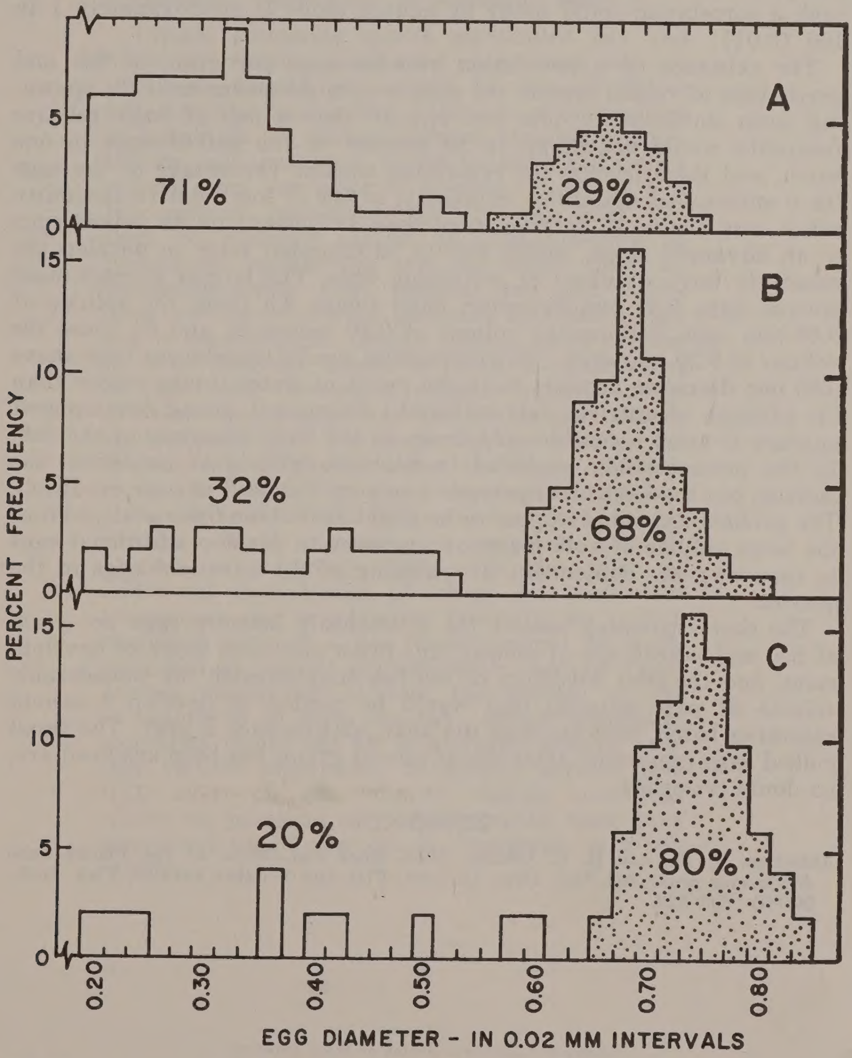

FIGURE 3. Frequency distributions of yolked eggs found in three different hake ovaries illustrating differences in ratios between small yolked and advanced yolked eggs.

represents an intermediate value, 221 eggs per gram of fish, and the 1:0.25 ratio (Figure 3C) a high value, 324 eggs per gram of fish. If total eggs are considered, the eggs per gram of fish are relatively much closer—315, 327, and 403, respectively.

The advanced group of eggs made up 50 percent or less (17–50 percent) of the total number of yolked eggs in 10 hake, and 51 percent or more (51–83 percent) in 12 hake. None of the hake in the first group had as many as 175 eggs per gram of fish, but 10 of the 12 fish in the latter group contained more than 175. The correlation coefficient between percentage of eggs in the advanced mode (X) and advanced eggs per gram of fish (Y) ($Y_c = 36.4 + 3.04X$) is 0.53; the probability that such a correlation could occur by chance alone is approximately 1 in 100 (0.01).

The existence of a correlation between eggs per gram of fish and percentage of yolked eggs in the advanced mode makes multiple spawning seem unlikely. It does not appear that a fish of high relative fecundity would spawn up to 83 percent of the yolked eggs in one batch, and then develop the remaining smaller percentage of the eggs for a subsequent spawning. Similarly, a fish of low relative fecundity which was unable to develop more than 17 percent of its yolked eggs to an advanced stage, would hardly be expected later to develop the relatively large numbers of remaining eggs. The largest average-sized opaque eggs, 0.80 mm diameter, have almost 2.5 times the volume of 0.60 mm eggs, 8 times the volume of 0.40 mm eggs, and 64 times the volume of 0.20 mm eggs. (The increase in size of translucent eggs above 0.80 mm diameter appears to be the result of water intake rather than the addition of nutrient yolk material.) In general, gonad development appears to exert a considerable drain on the body resources of the fish. In the present study, material to establish criteria of condition was lacking, but the hake all appeared to be very thin and in poor condition. The probability would appear to be slight that these fish could produce the large volume of yolk material necessary to develop additional eggs to spawning size subsequent to spawning of the advanced eggs in the ovaries.

The short spawning season, the relationship between eggs per gram of fish and percentage of yolked eggs in an advanced stage of development, and the poor condition of the fish coupled with the considerable volume of yolk material that would be needed to develop a second spawning batch, indicate that the hake spawns once a year. The small yolked eggs remaining after the advanced group has been spawned are, no doubt, resorbed.

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JOHN J. MAGNUSON, Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

Continuous locomotion in scombrid fishes.

Typical swimming speeds maintained day and night by various scombrids rangs from one to two body lengths per second for fish of 35 cm fork length. Among the functions of locomotion in scombrids are maintenance of hydrostatic equilibrium, gill ventilation, search for food, and simply moving from one place to another. Only the first two require continuous activity. At least two lines of evidence suggest that maintenance of hydrostatic equilibrium sets the lower limit on swimming speed. First, pectoral fins (the hydrofoils) are almost always extended and the mouth gap is usually slight (Pacific bonita, *Sarda chiliensis*, even close the mouth as much as 42 per cent of the time). Second, a negative relation exists between typical speed and the size of gas bladder and pectoral fins. The larger the gas bladder the less the fish weighs in water; the larger the pectorals the less is the speed required to generate given amounts of lift. Many species have no gas bladder. It is interesting to speculate how its absence in a pelagic fish, with the price of additional expenditures of energy for continuous locomotion, can be adaptive. Near the sea surface scombrids without a gas bladder might be more successful in pursuit of prey fishes, because rapid ascents would not increase the volume of gas so rapidly as to harm the fish. Deeper swimming scombrids would not be so hindered because sudden vertical movements at greater depths have little effect on gas volumes. Species that feed wholly on plankton or typically pursue their prey downward would also not be hampered by a gas bladder.

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Anim. Behav., 1966, **14**, 54–67

COURTSHIP, LOCOMOTION, FEEDING, AND MISCELLANEOUS BEHAVIOUR OF PACIFIC BONITO *(SARDA CHILIENSIS)**

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Generalizations in biology are often hampered by absence of knowledge about species and environments which are difficult to study in the laboratory. In the field of fish behaviour the lack of knowledge about the larger pelagic schooling fishes, such as the scombrids, forms a considerable gap in scientific experience. There are few studies on the behaviour of captive scombrids, and fishes of the open ocean are difficult to observe and study closely at sea (Magnuson, 1963). No studies have been made of the courtship behaviour of scombrids; indeed, they and other pelagic schooling fishes have often been assumed to have no discrete courtship behaviour and no pairing (Norman, 1948; Shaw, 1962).

Establishment of Pacific bonito (*Sarda chiliensis* (Cuvier)) in captivity at Marineland of the Pacific, Palos Verdes, California, has provided a unique opportunity to study courtship behaviour and other behaviour never before recorded in the literature for any scombrid fish. Large tanks such as the one at Marineland are the only ones available today which begin to simulate, even to a small degree, the dimensions of the pelagic oceanic environment.

The purposes of this study were to (1) describe swimming, feeding, courtship, and miscellaneous behaviour patterns of a pelagic schooling fish, *Sarda chiliensis*, (2) point out changes in some behaviour patterns during the day and before and after a meal and, (3) suggest the function of the behaviour patterns. Locomotion and feeding are considered first because they contain material that adds to the understanding of the sections on courtship and miscellaneous behaviour.

Materials and Methods

Observation Tank and Specimens

Observations of the behaviour of *S. chiliensis* were made at the oval fish tank at Marineland of the Pacific, Palos Verdes, California, in July 1962, May 1963, and March 1964.

The tank (Fig. 1) is 33 m long and 16·3 m wide from 0 to 4 m beneath the surface, and 27 m

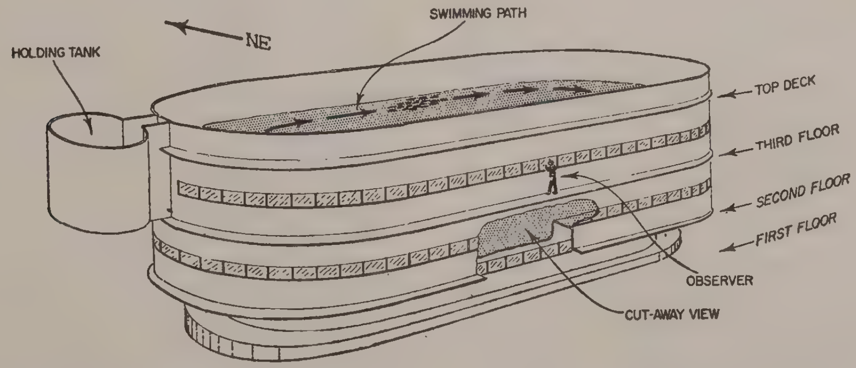

Fig. 1. Diagrammatic view of the oval fish tank at Marineland of the Pacific Floors, supporting structures, and outer walls not shown.

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*Contribution No. 17, Marineland of the Pacific Biological Laboratory.

long and 10 m wide from 4 m beneath the surface to the bottom. Fish could be observed through 170 windows, which were 1, 4, and 6·5 m below the surface and distributed around the periphery of the tank.

Sea water was pumped from a well on the beach at the rate of 1500–1800 l/min, and 9800 l/min were recycled through a series of filters. Water temperature was 22°C ± 1°. A concentration of 0·17 ppm, of copper ion reduced algal growth, parasite infestation, and disease. Horizontal visibility into the tank was normally over 15 m. Except for a clockwise eddy at the north-west end of the tank, water in the upper levels moved counterclockwise (mean speed = 10 cm/sec).

Sixty *S. chiliensis* were caught near Marineland of the Pacific in August 1961; about twenty-five survived and became established in the tank. After they learned to feed in captivity, the diet consisted of frozen smelt (Osmeridae). Of the original survivors, ten were still alive in October 1964, after 38 months in captivity. During the first 9 months in captivity they grew from 45 or 50 cm to 57 cm in fork length. All *S. chiliensis* in the tank appeared to be about the same size. Three sampled in July 1962, averaged 56·8 cm (range = 55·7–58·8 cm) in fork length and 2·53 kg in weight.

The oval tank, part of a public display, presented circumstances which limited experimental manipulation of the species studied. More than 800 fish of over forty species resided in the tank. Five 15 min shows were presented daily during which divers fed the fish. *S. chiliensis* occasionally swam down and took some food from the divers, a behavioural trait that interfered with controlled feeding. Between the shows behaviour observations could be made with little interference and prior to the 10 o'clock opening there was no public or diver interference. Captive fishes appeared habituated to show announcements and background music as well as to sounds made by tapping on the tank windows and sides.

Observation Methods

Typical swimming speeds were calculated from the time it took a fish to swim a given distance. The *S. chiliensis* usually swam a straight course 1–2 m from the 1 m deep windows and the observer could walk abreast of the fish as it swam along. In July 1962 data were recorded for a fish on the same side of the tank as the observer over a 7·2 m distance. Tail beats were counted at the same time. In May 1963 data were recorded from fish on the side of the tank opposite the observer over a 3·7 m distance. Depth of swimming was obtained by noting the position of the fish relative to the wall, which was marked at 0·5 m intervals below the water surface. Higher speeds, when the fish were stimulated with food, were recorded on 16 mm motion picture film with a stationary camera at 48 and 64 frames per second. The progression of a fish from frame to frame was measured later on a film editor in terms of body length and then corrected for direction and speed of the water currents. Tail beats were also counted from the motion picture projection.

Two methods were used to measure the frequency of each behaviour pattern. In July 1962, a stationary observer counted each behaviour pattern for all *S. chiliensis* swimming by the window from right to left over a 10 min period. He was stationed at a window on the 1 m level halfway down the southwest side of the tank (Fig. 1). The proporton of fish with their mouths closed was determined by counting those with closed mouths and those with open mouths as the school swam by. In May 1963, an observer watched only one fish and walked past the 1 m windows at such a speed as to stay adjacent to that particular fish. Since the corridor of 1m windows does not extend completely around the tank, on the average only 71 sec of continuous observation could be made.

Variations in a striped coloration on the flanks of the fish made possible identification of individuals at large in the tank. The parallel stripes were longitudinal or oblique in a posterior dorsal axis. This parallel pattern was sometimes compounded by branched forks oriented anteriorly or posteriorly. Some stripes were broken or even existed as a series of dashes.

The large size of the tank and the speed of the fish during courtship or feeding made it impossible to keep numerical data on the sequences of these behaviour patterns.

Observation Schedule

In July 1962, observations were made at eight periods of approximately 1·5 hr intervals from 08.00 until 19.00 hours. These usually were made while the divers were not in the tank. Each period included three 10 min behaviour observations by a stationary observer and nine estimates of typical swimming speed, tail-beat frequency, and percentage of fish with closed mouths. On three observation days (July 17, 19 and 20) *S. chiliensis* were fed as many osmerids as they would eat at 09.00 and 15.00 hours. On 2 days (July 16 and 18) they were not fed during the observation period.

In May 1963, swimming speed and depth were recorded on four mornings from 06.30 to 11.30 hours. Also in May 1963, behaviour observations were made separately on eleven individual fish on four mornings between 07.00 and 11.00 hours. Each fish was observed for approximately 3 min during every 30 min period. In one treatment the fish were fed all they would eat at 06.30 hours, and in a second treatment they were not fed. *S. chiliensis* occasionally took food from the divers. It could be assumed, however, that on a not-fed day a fish had not eaten since the last show of the previous evening.

Locomotion

S. chiliensis swam continuously, usually with pectoral fins extended, pelvic fins and first dorsal fin appressed, and mouth agape at an angle of 10–15 degrees. Direction of swimming was against the current. Their average speed, during July 1962, when not feeding or courting, was 88·2 cm/sec at a tail-beat frequency of 1·42 beats/sec (n = 324 observations). The average or typical speed remained fairly constant through the day and observation indicated that speeds at night were similar to the typical day speeds. Assuming that they maintain this average during the hight, about 69 km would be travelled in a 24 hr period.

The typical speed (Fig. 2), measured as the modal value in May 1963, was the same for fish at different depths, 70–79 cm/sec, yet the proportion swimming faster than the modal speed was greater for the shallow depths.

Continuous swimming of scombrids functions both in gill ventilation (Hall, 1930) and apparently in maintaining swimming depth. This species does not have a gas bladder and is more dense than sea water. At the typical speeds the pectoral fins were almost always extended and had a positive angle of attack. As the fish swims, lift would be expected from the planing action of the pectoral fins. Lift received while swimming at the modal speed of 70–79 cm/sec was apparently sufficient to oppose the weight of the fish in sea water. This speed was apparently more than sufficient for gill ventilation because, as will be pointed out below, *S. chiliensis* often swim with their mouths closed.

Swimming speeds and tail-beat frequencies were measured for a range of speeds. The linear regression of body lengths per second (y) on tail beats/sec (x) was calculated, $y = 0{\cdot}4905 + 0{\cdot}6394\ x$, and presented graphically in Fig. 3 (n = 31 observations, 95 per cent confidence interval, $b = 0{\cdot}639 \pm 0{\cdot}168$, $y = 2{\cdot}459 \pm 0{\cdot}231$; $s_x = 1{\cdot}291$, $s_y = 1{\cdot}004$, $s_{yx} = 0{\cdot}582$).

The most rapid swimming observed was 6·5 body lengths/sec, or about 370 cm/sec. Reports

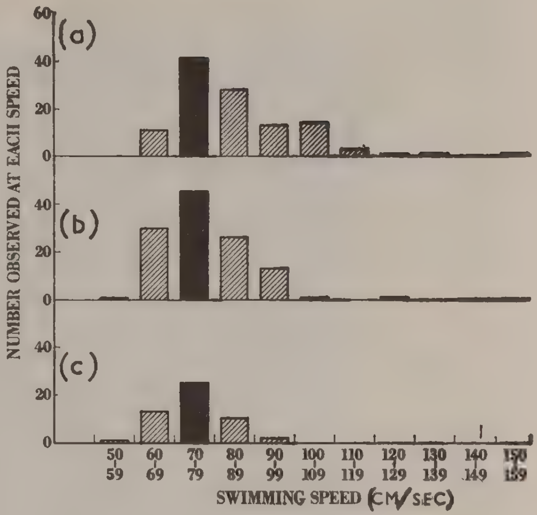

Fig. 2. Relation between swimming depth and swimming speed. Modal class interval shaded black. Swimming depths: (a) 0–1·2m; (b) 1·3–2·2m; (c) 2·3–3·8m.

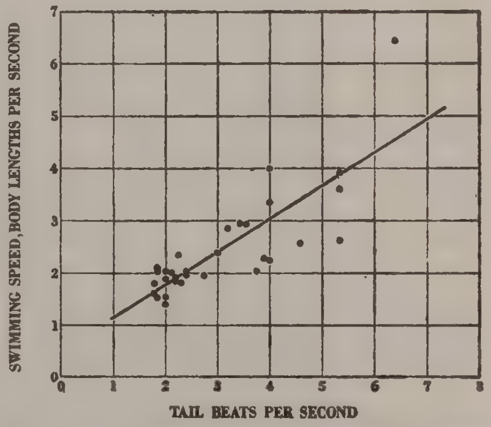

Fig. 3. Relation between swimming speed and tail beats/sec.

for skipjack tuna (*Katsuwonus pelamis* (Linnaeus)) at sea about the same size as *S. chiliensis* were as high as 640–770 cm/sec (Watanabe, 1942) and about 570 cm/sec.* *S. chiliensis* also swam more slowly than *K. pelamis* and yellowfin tuna (*Thunnus albacares* (Bonnaterre)) at the same tail-beat frequency. At four tail beats/sec *S. chiliensis* 57 cm in fork length travelled only 170 cm/sec, whereas *K. pelamis* 57 cm in fork length averaged 230 cm/sec (Yuen, MS.) and *T. albacares* 52 cm in fork length averaged 240 cm/sec (Yuen, MS.). Apparently *S. chiliensis* are less powerful swimmers.

Feeding Behaviour

S. chiliensis was the first species to reach and ingest the food tossed onto the surface, even though Pacific barracuda (*Sphyraena argentea* Girard), yellowtail (*Seriola dorsalis* (Gill)), and tarpon (*Megalops atlantica* Valenciennes) were also in the tank and ate osmerids. The other species were able to eat a higher percentage in the latter part of the feeding period as the *S. chiliensis* became satiated. The high speed of *S. chiliensis* gave them an advantage over the other species in a 'scramble' type of competition.

While feeding, *S. chiliensis* accelerated rapidly towards the dead osmerid and either took it headfirst into the mouth or crosswise in the jaws. A sidewise head movement coupled with a sudden deceleration enabled them to take crosswise prey headfirst into their mouths. Several sudden snapping movements of the jaws followed and were probably involved in swallowing the prey.

Schooling was disrupted with the introduction of food; in addition each fish underwent a change in coloration. The new coloration (Plate IV) consisted of nine or ten black, vertically oriented bars on the flanks superimposed over the typical colour pattern of diagonal stripes. A yellowish middorsal stripe also became intense from the tip of the snout to the base and sides of the first dorsal fin. The narrow stripe contrasted with the dark dorsal surface of the head and was very obvious in a feeding *S. chiliensis* viewed from the front. Both the vertical bars and middorsal stripe faded as the fish approached satiation, and the colour changes were not released in satiated fish by additional food stimuli. The barred pattern was observed in all feeding *S. chiliensis* and was also observed at the time of capture on hook and line at sea by Klawe (1961) and Walford (1937). The significance of this coloration will be considered in the section on courtship.

Courtship

General papers on spawning of pelagic schooling species have assumed that such fishes have no discrete courtship behaviour and no pairing (Norman, 1948; Shaw, 1962). Aronson (1957) argued that stimulation of spawning in 'school-breeding' fishes was of a general nature, whereas among other fishes the stimulation of one individual by another prevailed. Detailed studies of cod (*Gadus callarius* L.) by Brawn (1961) demonstrated definite courtship behaviour, pairing, and aggression. *G. callarius* previously were believed to shed eggs and sperm promiscuously while gathered in large active schools (Aronson, 1957). Simpson (1956) believed that, as more observations were actually made, temporary pairing and discrete spawning behaviour would be found in most fishes believed to spawn in schools.

Prior to the observations below on *S. chiliensis*, virtually nothing was known of courtship for any scombrid. It is possible that some of the poor biting *K. pelamis* schools described by Tominaga (1957) were spawning. He wrote of *K. pelamis* schools without regular ranks, often called 'playing schools'. Such schools were also called 'jumpers' or 'flashers' and did not bite well when fished by Japanese pole-and-line fishing boats. Tiews (1963) believed that fragmentary field observations on bluefin tuna (*Thunnus thynnus* (Linnaeus)) reported by Sella (1911) and Heldt (1932) indicated that some form of pairing did occur.

In July 1962, eighteen of the twenty-two *S. chiliensis* in the oval tank were identified by variations in their diagonally striped colour patterns. Eight exhibited an exaggerated wobbling type of swimming and nine exhibited a following behaviour (see below). One other was recorded to exhibit both types of behaviour, but this could have resulted from a misidentification. Although there were no apparent external anatomical differences between the sexes, the dimorphism in behaviour distributed 50–50 among the fish suggested that these patterns were a part of courtship. We postulated that 'wobblers' were females and 'followers' were males.

To obtain some verification of the apparent sexual dimorphism in behaviour, one identified

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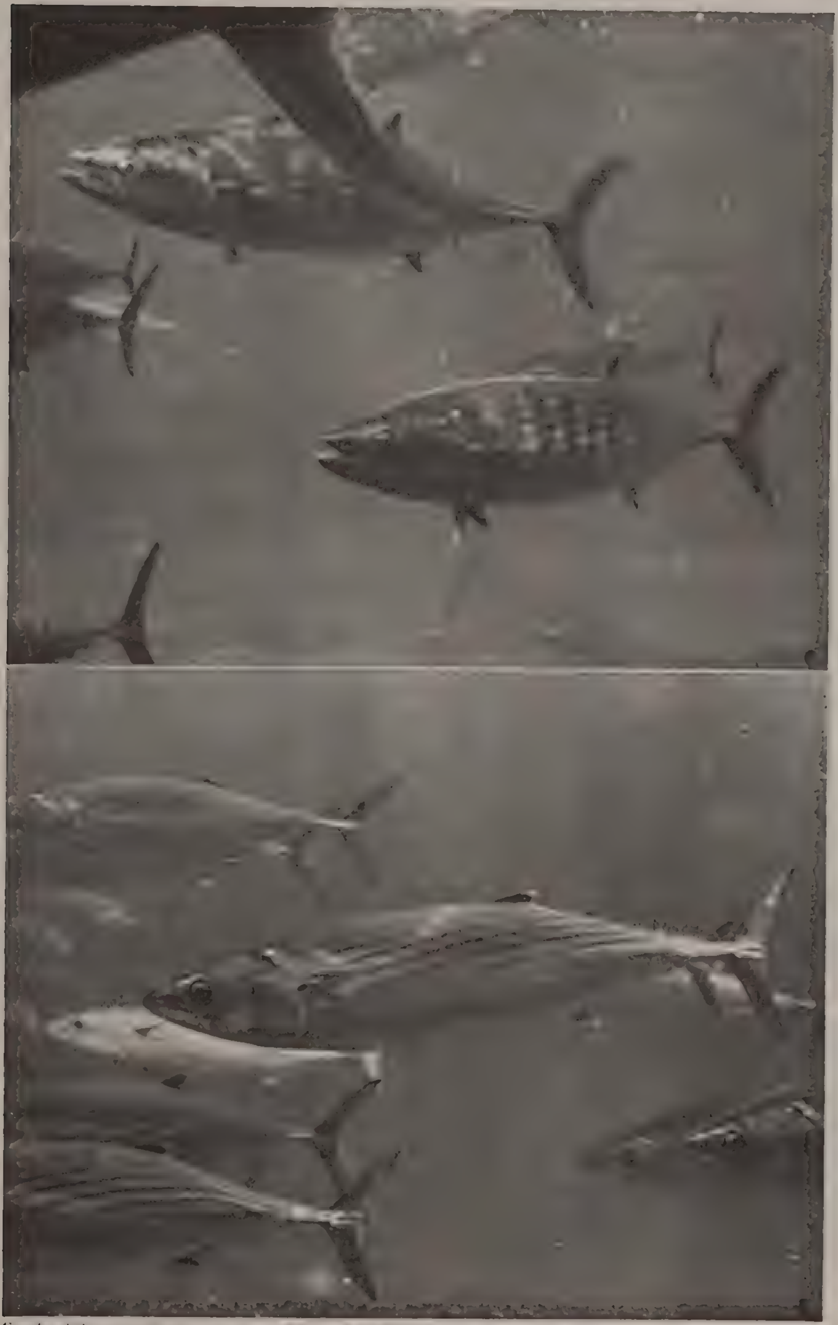
*Yuen, Heeny S. H., MS.: Swimming speeds of yellowfin and skipjack tuna. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii.

PLATE IV



Sarda chiliensis (a) with the transient vertically barred coloration and (b) without the vertically barred coloration.

'wobbler' and one identified 'follower' were speared from the population. Gonad identification agreed with the previous sexing by behaviour.

Some indication of the reproductive state was obtained by further examination of the gonads of these two fish plus those of another male speared from the tank that had not previously been identified as a wobbler or a follower. The weights of the males' testes were 1·5 and 3·8 per cent of their body weights. Some free milt was present. The weight of the female's ovaries was 1·6 per cent of its body weight. The largest modal group of ova diameters was 0·3 mm, and no free ova were in the lumen. A female *S. chiliensis* was caught at sea off Palos Verdes during the same week the above fish were speared. It also had ovaries weighing 1·6 per

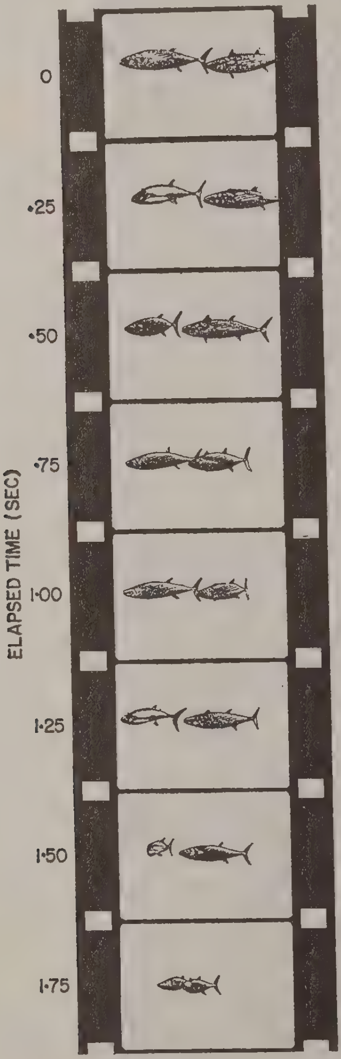


Fig. 4(b)

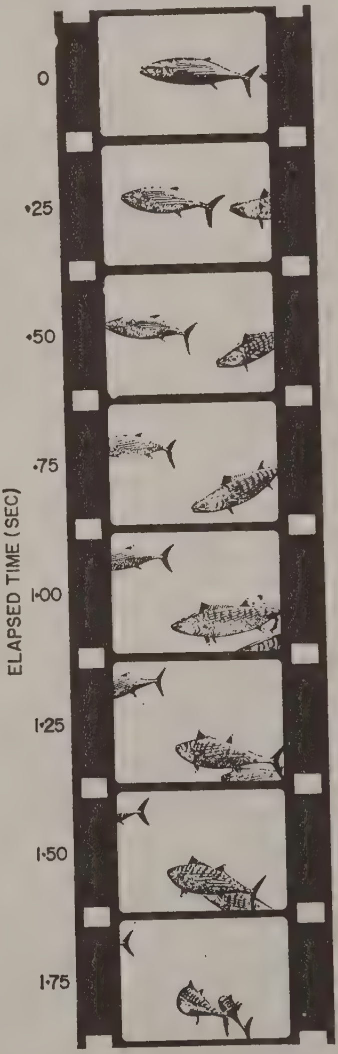


Fig. 5(b)

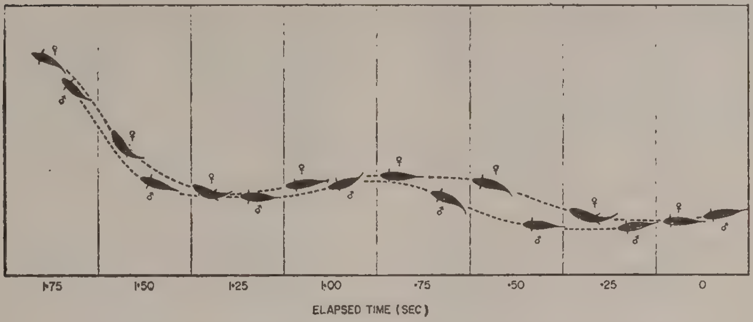


Fig. 4. (a) Wobbling by a female and following by a male as drawn from 16 mm motion picture frames (b), (left).

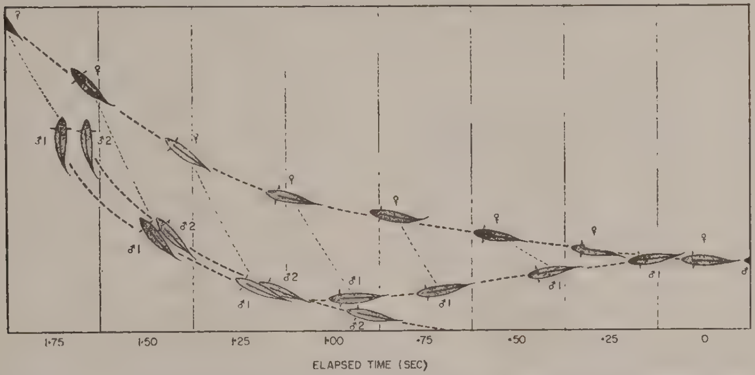


Fig. 5. (a) Lateral threat display by a male toward a second male as drawn from 16 mm motion picture frames (b), (left).

cent of its body weight and a modal group of ova diameters at 0·3 mm. Yet this female had forty free ova with a modal diameter of 1·5 mm in the lumen indicating spawning was primarily completed. Similarities between these two females suggest that the female speared from the tank may have recently terminated spawning. Gonad examination indicated that the main period of spawning had passed prior to the July 1962 observations.

Brief descriptions of behaviour patterns observed during courtship are presented below.

Wobbling ♀ (Fig. 4). When viewed from above, the path of the female forms a series of waves. At the outer extreme of each wave her body tilts inward 5–15 degrees from the vertical. The dorsal fin is depressed. Tail beats are more rapid than during typical swimming and have a very low amplitude. A complete wobble from left to right and back has a duration of approximately 1·0 sec and the overall appearance is a rapid, wobbling swimming motion.

Circle swimming ♀. The path of the female forms a tight circle about three body lengths in diameter usually just beneath the water surface or as deep as 4 m. Dorsal fin is depressed, the dorsoventral axis of the body is tilted slightly toward the centre of the circle, and no obvious colour change occurs.

Fleeing ♀. The female swims rapidly in an erratic course, usually darting away from a group of males that have been swimming just behind her. No obvious colour change occurs.

Tail nosing ♂. A male swims behind another fish, on occasion actually touching his nose to the caudal fin of the lead fish. During typical schooling, in contrast, the fish are usually more than one body length behind or off to one side, *Following* ♂ (Fig. 4). A male swims immediately in tandem behind a wobbling female and maintains a typical swimming motion. His path follows that of the female; however, his body does not tilt from the vertical as does the female's, and tail nosing sometimes occurs. The vertically barred coloration described for feeding *S. chiliensis* is present in some cases, absent in others.

Circle swimming ♂. A male with or without the vertically barred coloration swims rapidly in tandem several centimeters behind a circle swimming female. Sometimes the male's snout is as far forward as the insertion of the female's first dorsal fin, but he does not swim alongside the female in a vent to vent position. The dorsal fin is extended, and the dorsoventral axis of the body is normal to the water surface.

Lateral threat display ♂ (Fig. 5). Coloration of a male in the following position changes to an intense, vertically barred pattern including the middorsal stripe. The first dorsal fin and pectoral fins are extended, swimming speed decreases, and the lateral surface of the body is displayed to another male, also in the following position. During the display the first male usually banks toward the second, approaching it laterally in a parallel swimming position almost to within a pectoral fin length. Physical contact between the two males does not occur. The second male also has the vertically barred pattern, middorsal stripe, and erected dorsal and pectoral fins.

Positioning ♂. A male, behind a wobbling or fleeing female with one or more other males, swims in a dodging path in such a manner as to bring him to the following position immediately behind the female. The other males, each with vertically barred coloration, swim in the same way and form a group of fishes swimming under, over, and around each other in a generally parallel course behind the female.

A typical sequence of the above patterns was tail nosing by a male, wobbling by a female, following by the male, and circle swimming by both. Another common sequence was tail nosing by a male, wobbling by a female, following by more than one male, lateral threat displays and positioning by the males, and occasionally fleeing by the female. Sometimes tail nosing was absent and the sequence was initiated by wobbling or following.

Males tail nosed females, other males, and even another species, blacksmith (*Chromis punctipinnis* (Cooper)). When a male *S. chiliensis* or *C. punctipinnis* was tail nosed, it darted rapidly away or swam along without altering its behaviour. In either case the tail nosing male stopped following the lead fish within a few seconds. If the tail nosed fish was a female *S. chiliensis*, wobbling was often released. If wobbling occurred, the male continued to follow the female. Apparently a male was unable to identify the sex of another *S. chiliensis* except by behavioural characteristics. Occasionally wobbling occurred without a male in the following position, but a male usually swam over and began following.

If only one male was following a female, circle swimming by both occasionally occurred. The transition from wobbling to circle swimming was gradual, with the wobbles becoming more and more pronounced until the female continued one phase of the wobble into a circular path instead of turning back to the next phase of the wobble. A courting pair also swam at a slightly faster speed than the main school, and by the time circle swimming occurred they were temporarily separated from the school. The gametes were released during circle swimming. In the July 1962 observations, milt was observed being released once, but during March 1964, both eggs and milt were frequently observed being released throughout periods of circle swimming which lasted as long as 20 sec.

The importance of the reciprocal stimulation between individuals in the formed pair was evidenced in that the courtship sequence did not continue to the later stages unless pair formation was maintained. If two or more males followed the female, the males became involved in lateral threat displays. If they dropped back several meters behind the female, she stopped wobbling but resumed as soon as any one of the males returned to the following position. Aggressive bouts were usually long and included positioning as well as lateral threat displays. Positioning did not result in the males falling back behind females. As the number of positioning males increased the female often began fleeing as if attempting to get away from the group behind her. A courtship sequence often ended at this point and seldom resulted in circle swimming without regressing to the initial steps in the sequence. Numerical evidence for this observation was also found in the analysis of frequency data below.

Numerical data on courtship were provided by the frequencies of wobbles, follows, circle swims, and aggression (lateral threat displays plus positioning) observed in 10 min periods during July 1962.

The frequency of each courtship element was summed across all 10 min observations made during the height of this activity (12.00–18.00 hours). The most frequent behaviours observed in these 520 min were following, with a total frequency of 392, and wobbling, with a frequency of 318. Successively less common behaviours, dividing follows into two groups, were follows by males with the vertically barred pattern, 255; follows by males without the vertically barred pattern, 137; lateral threat displays plus positioning, 42; and circle swimming, 31. Those behaviours occurring earlier in the courtship sequence, such as wobbles and follows, were more common than those occurring later in the sequence, because most initiated sequences did not continue to the later stages.

Spearman rank correlation coefficients for each pair of courtship movements were positive and significant ($P \leq 0{\cdot}05$) (Table I). Forty of the 111 10-min observations contained no courtship, and the 100 per cent positive correlations indicated only that all courtship elements tended to occur together. Observations with zero frequencies of any two courtship elements were eliminated, and r_s between those two elements was recalculated. They ranged between $r_s = +0{\cdot}868$ and $r_s = -0{\cdot}016$ (Table I). Apparently the greatest association was between the frequencies of wobbles and follows (Fig. 6), while the lowest association was between circle swims and aggression (Fig. 7). Even after the zero-zero observations were eliminated, five of the six coefficients were positive and significant ($P \leq 0{\cdot}05$). The $r_s = -0{\cdot}016$ between circle swimming and aggression was not significantly different from zero. Since wobbles and follows were each positively associated with both circle swimming and aggression, the lack of association between circle swimming and aggression indicates an antagonistic relation between the latter. The correlation of observed frequencies was not a powerful tool in an analysis of courtship sequences. Yet the single low coefficient provided some numerical verification for the observation that aggression interrupted the courtship sequence, preventing the succession to the circle swimming stage.

Table I. Spearman Rank Correlation Coefficients Between the Frequencies of Courtship Behaviour Patterns Observed During 10 min at the Oval Tank by a Stationary Observer in July 1962

Behaviour patterns	Sample includes all 10 min observation periods			Sample includes only those 10 min periods which contained at least one of the two correlates		
	r_s	n	t	r_s	n	t
Wobbles × follows	0·879	111	19·222*	0·868	70	14·398*
Wobbles × circle swimming	0·534	111	6·600*	0·510	66	4·741*
Wobbles × lateral threat + positioning	0·598	111	7·784*	0·602	66	6·029*
Follows × circle swimming	0·597	111	7·764*	0·571	57	5·154*
Follows × lateral threat + positioning	0·680	111	9·687*	0·735	57	8·035*
Circle swimming × lateral threat + positioning	0·590	111	7·628*	−0·016	25	0·075 ns

*Significant at $P \leq 0{\cdot}05$; ns, not significant at $P \leq 0{\cdot}05$.

The actual releasers in the courtship sequence were not determined in the present study. Evidently tail nosing or following by a male released

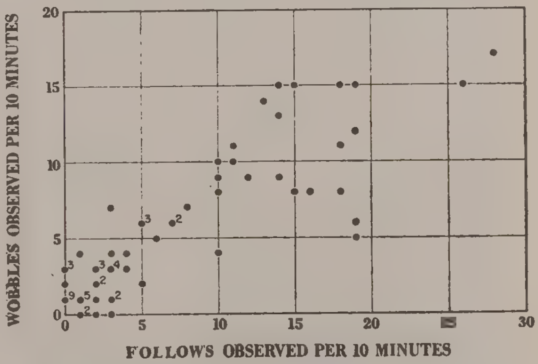


Fig. 6. Relation between frequencies of wobbles by females and follows by males observed by a stationary observer during 10 min periods. Numbers refer to multiple occurrence of identical values,

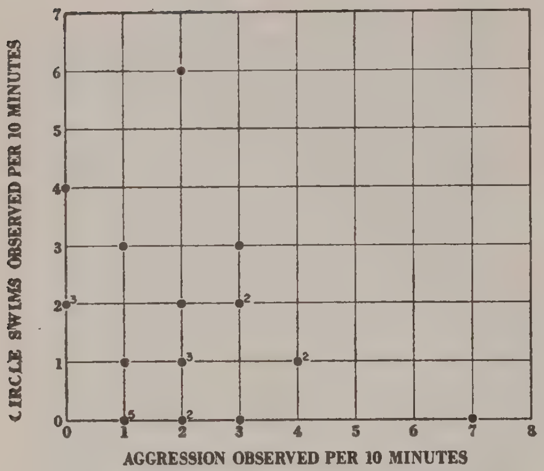


Fig. 7. Relation between frequencies of circle swims and aggression (lateral threat displays plus positioning) observed by a stationary observer during 10 min periods. Numbers refer to multiple occurrence of identical values.

wobbling by the female, and wobbling by the female likewise released following by the male. The presence of a second male released aggression in the form of lateral threat displays. What aspects of the wobble and follow release circle swimming and then the release of gametes was not clear. In addition to the position and movement of the fish, coloration such as the transient middorsal stripe, transient vertical bars, the dark dorsal fin, and the white tips of the anal fin and second dorsal fin, plus olfactory stimuli, may be involved at some points in the sequence.

The occurrence of the transient, vertically barred coloration among males during agonistic bouts associated with courtship provided some insight to the appearance of the same coloration in both sexes during feeding. The intensity of the bars was greater during the lateral threat displays to other males than ever observed for a solitary male following a wobbling female. The coloration plus the display of the dark first dorsal fin definitely appeared to be a part of the lateral threat display. An intensified vertically barred coloration was also characteristic of aggressive behaviour among males of the nandid fish *Badis badis* (Hamilton-Buchanan) (Barlow, 1963). Since aggression has often been associated with feeding, even among immature fish (Magnuson, 1962), it may be that the vertically barred coloration during feeding was also a lateral threat display. Perhaps the colour change while feeding has acquired a secondary significance of indicating the presence of food to other members of the school, as suggested by Nakamura & Magnuson (1965).

In summary, three divisions can be distinguished in the courtship of *S. chiliensis*: (1) pairing (probably only temporary), (2) defence of a female or the right to fertilize ova, and (3) a sequence of behaviour leading to a simultaneous and adjacent release of gametes. In regard to the adjacent release of gametes, swimming in tandem over and over again in the same small circle while spawning would appear to enhance the probability of fertilization.

Miscellaneous Behaviour

In addition to swimming, feeding, and courtship movements, *S. chiliensis* had at least nine other individual behaviour patterns. These patterns were named mouth closure (long), mouth closure (short), snap, yawn, lean, bend, jerk, quick swim, and defecation. A brief description of each movement is given below.

Mouth closure (long). The mouth and gill clefts are completely closed from 1 to more than 15 sec, then reopened slowly to the typical swimming posture. Locomotion is maintained with no apparent change during the closure.

Mouth closure (short). The mouth and gill clefts are closed and suddenly reopened to the typical posture within a 1 sec period.

Snap. The mouth is quickly opened from the typical position to an angle approaching 70°, and immediately closed and reopened to the typical gape. Gill covers are flared and first dorsal fin extended during the snap.

Yawn. The mouth is slowly opened to an angle approaching 70° and, at the same time, the gular region is depressed, gill covers are flared, first dorsal fin and pelvic fins are extended, and caudal movement is stopped. Then posture more rapidly returns to that of typical swimming. In extreme yawns the fish begins to sink tail first.

Lean. The body slowly tilts to the left or right side until the dorsoventral axis in extreme cases is parallel to the water surface. In a right lean, the left pectoral fin and left pelvic fin are extended while the right ones are depressed, and vice versa for a left lean. If the lean exceeds an angle of approximately 45° from the vertical, the first dorsal fin is often extended. In extreme leans caudal fin movement usually ceases, and the fish sink slowly. Leans have some tendency to occur during gradual turns, *Bend.* The body is flexed laterally until the anterior–posterior axis forms a shallow U. The mouth is closed completely just before the bend and is not reopened until the bend or series of bends is completed. Typical tail-beat frequency is interrupted.

Jerk. A sudden twitch or quiver passes over the body from head to tail in a single rapid movement. Typical swimming movements are not disrupted, and no acceleration occurs.

Quick swim. A rapid acceleration followed by a cessation of all caudal movement results in one fish leaving the rest of the school far behind.

Defecation. Defecation results in the discharge of a cloud of a flocculent white fecal material. No obvious external body movement is associated with defecation.

From the observations made in May 1963, it was possible to calculate the frequency of each miscellaneous behaviour per fish per unit time (Table II). An average of 18·7 min of observation was made for each fish at each treatment (fed or not fed). Some miscellaneous behaviour patterns were extremely rare, such as the quick swim, 0·2 fish per 10 min, and the jerk, 0·1 per fish per 10 min. Others, such as the mouth closure (long), 7·6 per fish per 10 min, and mouth closure (short), 1·5 per fish per 10 min, were second in frequency only to movement of the trunk and caudal fin during locomotion. Considering all miscellaneous behaviour patterns as a group, the frequency was almost twenty per fish per 10 min.

These behaviour patterns often occurred in rapid sequence (within 2 sec of each other). Twenty-five per cent of the July 1962 sequences contained three or more movements. Some became somewhat complex, such as bend-lean-bend-jerk, lean-bend-lean-bend-bend, lean-yawn-snap-bend, bend-bend-bend-bend-bend, etc. Similar sequences were observed in May 1963.

The functions of these miscellaneous movements are difficult to determine. Movements similar to those listed for *S. chiliensis* have often been grouped as comfort movements. A reason given by Baerends & Baerends von Roon (1950) for calling them comfort movements was 'it looks as though these behaviours make the fish more comfortable'. This reason seems inadequate as evidence and miscellaneous behaviours should be considered more critically as movements possibly associated with some vital processes of the animal. An attempt is made below to suggest the function of the various miscellaneous movements of *S. chiliensis*.

Mouth closure (long) may be associated with olfaction, gill ventilation, or both.

Any opening movement of the jaws of *K. pelamis* would be expected, on the basis of an

Table II. The Average Frequency of Miscellaneous Behaviour Patterns Listed in Order of Commonness in May 1963 and the Difference in the Average Frequency of Each Among Fish Fed Within 4 hr and Fish Not Fed for at Least 12 hr

Behaviour patterns	Average frequency per fish per 10 min for both treatments	Fed treatment (0–4 hr after meal)	Not-fed treatment (at least 12 hr after meal)	Fed minus not-fed difference
Mouth closure (long)	7·6	3·5	11·6	− 8·1*
Mouth closure (short)	5·0	4·6	5·4	− 0·8 ns
Lean	2·4	2·9	2·0	+ 0·9 ns
Bend	1·8	2·6	1·1	+ 1·5*
Yawn	0·6	0·9	0·4	+ 0·5*
Snap	0·4	0·5	0·3	+ 0·2 ns
Defecation	0·2	0·3	0·2	+ 0·1 ns
Quick swim	0·2	0·2	0·2	0·0 ns
Jerk	0·1	0·2	0·0	+ 0·2 ns
Total	18·3	15·7	21·2	

*Values of *T* for Wilcoxon matched-pairs signed-rank test (Siegel, 1956) significant at $P \leq 0·05$ with a sample size of eleven fish; ns, not significant at $P \leq 0·05$.

anatomical and experimental study by Gooding (1963), to draw water through the anterior nares over the rosettes. Movements of carmine particles and various dyes near the nares of living fish have demonstrated that water movement through the olfactory capsule is brought about by the respiratory movements of the jaws in a variety of teleosts (Johnson & Brown, 1962; Liermann, 1933; Pipping, 1927; Parker, 1911). Pipping (1927) noted that whenever water movement in and out of the olfactory capsule was associated with respiratory movements, subsequent sectioning revealed accessory sacs in that species. Scombrids examined by Gooding (1963) and Iwai & Nakamura (1964) have accessory sacs. Apparently water is drawn into the olfactory capsule in live scombrids by movements of the jaws.

The higher frequency of mouth closure (long) among *S. chiliensis* not recently fed (Table II) might indicate that the mouth closure (long) was a method of sampling the environment for food odours, analogous to a 'sniff' among mammals, and may be a part of appetitive feeding behaviour. Scombrids have been shown by their responses to food extracts to have an effective sense of chemoreception (Tester, 1959). Intermittent flow of water over the rosette might be an advantage if fish are less able to detect continuous than intermittent odors. Adrian & Ludwig (1938), working with nervous discharges in the olfactory tract of catfish and tench, reported that during a 5–20 sec interval after a strong olfactory stimulus the organ was insensitive to further stimulation. An occasional sampling of a possible odor might tend to prevent such insensitivity of the olfactory organ or wasted movements during an insensitive interval.

Most of the above arguments on the possible olfactory role of mouth closure (long) also would apply to the other movements of the jaws, such as mouth closure (short), yawn, and snap. Pipping (1927) believed that yawning and snapping were olfactory reactions to hidden food. Yet none of these were shown to be statistically more common among *S. chiliensis* not recently fed than among those recently fed.

A second possible function of mouth closure (long) was associated with gill ventilation. Since the duration of time the mouth was closed would alter the amount of water contacting the gill filaments and possibly the amount of oxygen absorbed, variations in the frequency of mouth closure (long) might be geared to the oxygen demands of the fish. Saunders (1963) found that oxygen consumption for Atlantic cod (*Gadus morhua* Linnaeus) was greater after the fish had eaten than after a period of food deprivation. Similar results have been found with other fishes (Beamish, 1964). If *S. chiliensis* controls gill ventilation by altering the time its mouth is closed, the lower frequency of mouth closure (long) movements observed among recently fed fish in Table II is not unexpected.

The influence of a meal on mouth closure was studied in more detail by examining the percentage of fish that swam by with their mouths closed. The percentage with closed mouth was a rough estimate of the percentage of time each fish kept its mouth closed. This percentage has been plotted against time of day, on days when the fish were not fed, and on days when they were fed at 09.00 hours and 15.00 in July 1962 (Fig. 8). Each point represented eighteen to twenty fish passing the observer. Even though the variation was large, it can be seen that the percentage with closed mouth decreased after both the 09.00 and 15.00 hours feeding, and that the portion with closed mouth was much higher on the not fed than on the fed day. In *S. chiliensis* the observed decrease of mouth closure (long) movements (increase in time mouth is open) following a meal would result in more water passing over the gills at a time when oxygen consumption would be expected to be higher.

In conclusion it seems probable that mouth closure (long) was associated with both olfaction and gill ventilation. The extent to which the frequency and form of the movement were determined by each functional aspect was not clear.

A yawn looked like a stretching movement and has been considered as a displacement activity by Forselius (1957). Yet there are a number of other possibilities such as cleaning gill rakers or gill filaments, or even clearing the olfactory passages of mucus or debris. A yawn was almost always followed by a snap, which appeared identical to the food-swallowing movements. The filling of the mouth cavity with water and an immediate swallowing movement suggest that a yawn-snap could be involved in swallowing water. Another possible drinking behaviour was the quick swim-snap. Salt-water fish swallow water to replace that lost osmotically (Prosser & Brown, 1961). *Anguilla* sp. were reported to drink 40–225 ml/kg body weight per day (Smith, 1930). The yawn-snap and the quick swim-snap were the most likely move-

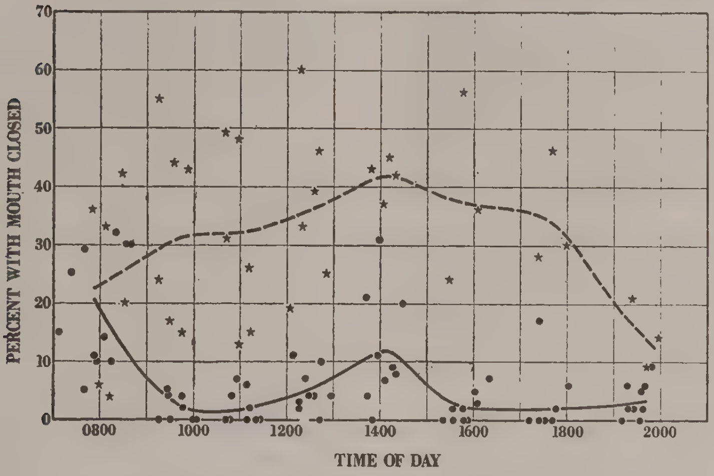


Fig. 8. Diurnal changes in the percentages of fish with mouths closed on days when they were fed (——) or not fed (– – –). Lines were drawn by eye through means for each 1·5 hr period.

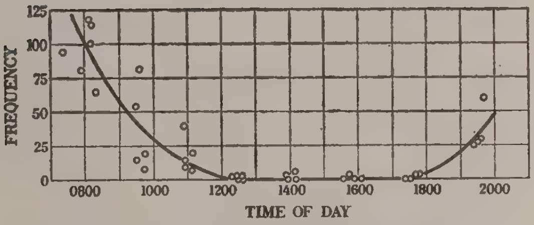


Fig. 9. Diurnal changes in the frequency of leans observed by a stationary observer over 30 min periods. Lines were drawn by eye through means for each 1·5 hr period.

ments involved in forcing water through the oesophagus and into the stomach in *S. chiliensis*.

Leans, although uncommon in May 1963, were the most common miscellaneous behaviour observed in July 1962. During a lean, *S. chiliensis* lost the effect of its countershading and reflected more light laterally through the water than in typical locomotion. In July 1962, leans were most common in early morning and late evening (Fig. 9). Leaning was also observed to occur at night. A possible function of leaning may be to help bring or hold a school together by making fish more visible to each other.

A possible function for bends and jerks may be associated with passage of material through the digestive tract. Bends were more common after a meal (Table II). A bend occasionally was followed by a jerk and, on several occasions, a fish which had bent and jerked was observed to defecate shortly afterwards. Also, the highest frequency of both jerks (four observed per 30 min of observation) and defecation (four observed per 30 min of observation) occurred between 2 and 3 hr after the 09.00 hours meal in July 1962. The average frequency of each in July 1962 was less than one per 30 min of observation. Considering the rarity of jerks and defecation, such isolated observations might be significant. Certainly more evidence is needed to prove or disprove a hypothesis that bends and jerks assist in the passage of material through the alimentary canal, but a suggestion to this effect existed in the data.

Summary

Establishment of Pacific bonito (*Sarda chiliensis* (Cuvier) in captivity at Marineland of the Pacific, Palos Verdes, California, has made it possible to study and describe in detail their swimming, feeding, courtship, and miscellaneous behaviours.

The oval tank in which the fish were kept was 33 m long, 16·3 m wide, and 11 m deep at the deepest point. Sea water was pumped from the ocean and was held at 22°C. Fish were viewed through 170 windows in the sides of the tank. The oval tank was part of a public display, a circumstance which limited experimental manipulation of the fish,

Swimming speeds and tail-beat frequencies were measured from movie films and direct observation. Frequencies of behaviour patterns were recorded either as the numbers observed among all fish by a stationary observer over 10 min periods or the number observed for a single fish for periods of time averaging 71 sec. With the latter method, data were kept separately for individual fish.

They swam continuously against the current at an average speed of 88·2 cm/sec and at a tail-beat frequency of 1·42 beats/sec when not feeding or courting. The linear regression of speed (y) in body lengths/sec on the number of tail beats/sec (x) was $y = 0{\cdot}4905 + 0{\cdot}6394\,x$ among feeding *S. chiliensis.*

When food (frozen osmerids) was tossed onto the surface, *S. chilensis* was the first species to reach and ingest it. During feeding, schooling was disrupted, and each *S. chiliensis* took on a vertically barred coloration and a yellowish middorsal stripe.

Courtship included temporary pairing, aggressive defense of females by males, and a sequence of behaviour leading to the simultaneous and adjacent release of gametes. A wobbling swimming motion by a female released a following by males, and likewise, if a male swam immediately behind a female, she began a wobbling type of swimming. Sexual discrimination was mediated by the wobbling and following movements. If more than one male was in the following position, agonistic behaviour occurred which included the transient vertically barred coloration observed in both sexes at feeding time. During courtship, only males assumed the coloration. Gametes were released during a circle swimming behaviour in which the female with the male in tandem swam in a circular path about three body lengths in diameter. If aggression occurred during the wobbling–following portion of the sequence, the sequence usually terminated and did not result in circle swimming and spawning.

S. chiliensis had nine miscellaneous behaviour patterns: mouth closure (long), mouth closure (short), snap, yawn, quick swim, lean, bend, jerk, and defecation. Often such movements have been considered as comfort movements, but in the present paper each was discussed separately in terms of association with some vital process of the fish. Mouth closure (long) movements may be associated with olfaction or gill ventilation; snaps following a yawn or a quick swim may be a drinking movement; leans may be a social releaser in schooling; and bends and jerks may be associated with passage of food through the alimentary canal.

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CENTRAL PACIFIC FISHERY RESOURCES: AN INTRODUCTION

By

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A minute or two after the plane leaves Honolulu International Airport, the island of Molokai comes into view. By the time the stewardess has passed out paper cups of pineapple juice, the island lies directly below. Its green northern cliffs jut steeply from the sea. The southern slope is gentler, falling gradually to a shore that from the air presents a curious appearance, for parts of it are edged by elliptical mud flats of unnatural symmetry. Sharply defined by the deep-water blue beyond, they look like regular reddish scallops on the land's green margin. For a moment they are puzzling. Then recognition comes: here are some of the oldest manmade structures in the United States.

These are ancient Hawaiian fishponds. Keone'o'io on Maui has been dated back to the mid-15th century, about the time Columbus was born. Some may be older. Others are certainly much more recent, for in the 19th century elderly Hawaiians testified they helped build them, at the behest of their chiefs. In the first exhaustive account of Hawaii's commercial fisheries (Cobb, 1905), 159 are listed; of these, 99 were still in use. As late as 1960 at least 10 were still in operation (Summers, 1964).

Walled by blocks of lava or coral, the fishponds enclosed several acres of shallow sea water. They were (and are) used primarily to raise the tasty mullet, which as fry enter the ponds through interstices in the walls or through barred gates and remain so long in the rich, protected ponds that they are unable to squeeze their way as adults to the open sea. Some ponds, such as those of the Hawaiian kings on Oahu, were used for the fattening of larger fish caught at sea.

Fish and poi were the principal Hawaiian foodstuffs. Once denigrated by Europeans, today they are recognized by physicians as constituting one of the most nourishing diets upon which mankind has luckily stumbled (Halford, 1954). They supported a race that was strong and graceful and, before the Europeans came, prolific; in 1778 that careful observer Captain Cook estimated the population of the islands at between 300,000 and 500,000. Recent authors tend to accept his lower figure (Hawaii, Department of Planning and Research, 1962). Even so, the islands, which in land area are about the size of Connecticut, had a population density approaching that of any of the better known centers of the New World. These figures mean that if the old Hawaiians ate no more fish per capita than do the citizens of the United States today (and it was probably much more) they would have taken a marine catch of about 3 million pounds a year. Three million pounds: this is just about what the Hawaiian longline catch amounts to today (Hida, 1966).

The fishponds, then, represent a most practical method by which the old Hawaiians, within the limits of a Stone Age technology, put the sea to work for them. Nor was their effort confined to the shore; then, as now, the skipjack tuna (aku) appeared in great numbers off the island shores in summer. Fleets of slender koa-wood outrigger canoes set out in pursuit of them. The Hawaiians had learned to lure the aku to their canoes by tossing shiny bait fish (small mullet, nehu, iao) in the water (Beckley, 1883) and this method is still followed in the commercial fishery. Today's aku fleet uses hooks of stainless steel. Not knowing metal and its uses, the Hawaiians patiently and beautifully crafted hooks (many still extant) of mother-of-pearl and of bone, choosing which they would use by the height of the sun and hence the reflectance of the hook.

The old Hawaiians put the sea to work because they had to. Not pressed so sorely for food, their successors, like most other peoples in our Western culture, have only laggardly recognized the gains that could come to them from the sea. Although Hawaii is the only State surrounded by the ocean, its commercial fish catch in 1964 was only about three times that of landlocked Arkansas (Lyles, 1966).

Which is not to say that commercial fishing is a dead or even moribund industry in Hawaii. It provides an ample living for several thousand modern Hawaiians. But certainly it has failed to keep pace with other elements of the State's booming economy. A generation ago, in 1940, Hawaii's total fish catch was 19,403,249 pounds, valued at about $1.5 million to the fishermen (Hawaii Territory, 1941). In 1965, it was 19,513,952 pounds, valued at about $3.6 million (Lyles, 1966). Taking into account the rise in the cost of living, the 1940 catch brought the fishermen the equivalent of $2.9 million 1957-59 dollars, the 1965 catch the equivalent of 3.3 million such dollars. Not much gain.

Hawaii at present has three products which are in national demand: sugar, pineapple, and charm. Sugar in 1965 brought in $176 million, pineapple $128 million, and the tourist industry $265 million (Bank of Hawaii, 1966). Eager to diversify its industry, and perhaps teased by the paradox of an island state that profits so little from its most abundant commodity--salt water--the leaders of Hawaii are looking more and more toward better use of the sea.

It was in this context that in May 1965, the Third Legislature asked Governor John A. Burns to convene a group of experts to survey the information on the fishery potentials of the central Pacific Ocean and offer guidance as to how Hawaii could make better use of them. The experts met. They sat in a bare and windowless conference room for 9 days. They considered all available scientific evidence concerning the principal commercial fishes of the central Pacific, the tunas. They reached conclusions. These conclusions and the evidence upon which they are based constitute this volume.

In a way, it seemed ironic that Hawaii should have convened an earnest conference on what was wrong with the State's fisheries when only a few weeks before the skipjack tuna fleet had ended the richest year in its history. In 1965, 16,157,309 pounds (7,327 metric tons) had been taken (Hawaii Fisheries, 1966). This was more than 2 million pounds over the previous record year, 1954.

And the skipjack tuna normally constitutes 66 percent of the Hawaiian catch by weight and 40 percent of its value to the fisherman (Uchida, 1966). Yet the aku fleet, with its 21 small vessels, and the longline fleet with 31, surely must be reaping only a small portion of the harvest of the central Pacific. To put some figures to the potential of that harvest was one of the chief objects of the conference.

Not so many years ago, some responsible scientists regarded the central Pacific Ocean as a marine desert. Its very color attested to impoverishment, for the deep burning blue that is characteristic of most of the area tells the trained observer that the water contains very little plankton, the floating plants and animals that are the first links in the food chain of the sea.

Two developments during the past 15 years have shown this picture to be drastically oversimplified. First, the Department of the Interior established a laboratory of its Bureau of Commercial Fisheries in Honolulu to study the fishery potentials of the central Pacific in more detail than ever before. That Laboratory has convincingly shown that this is no marine Sahara, largely devoid of animal life, but something that more closely resembles the high plains of east Africa, which may look bleak and barren to casual inspection but which support hordes of lions, wildebeests, and elephants.

The most profitable crop of the sea is the harvest of marine animals. Plunging steeply from volcanic crest to abyssal depths, Hawaii lacks the broad inshore banks from which such invertebrate animals as oysters and shrimps and many commercially important fishes are taken. But the central Pacific, although it has no extensive banks and its warm blue waters are indeed on the whole less rich than those of northern seas, is the habitat of the tunas, animals that in their freedom and power and speed might be called the marine equivalent of the lions of the east African veld.

Within a generation, Japan has been able to build a longline fleet that now ranges from shore to shore in three oceans, from Belém to Dakar in the Atlantic, from Durban to Perth in the Indian, from Hong Kong to Mazatlán in the Pacific. The tunas are its principal catch. Although the Japanese longliners are seen in every major warm-water port in the world, it is impossible to separate their total tuna catch by oceans. This obscurity is not deliberate, apparently, but lies in the traditional reporting systems of Japan. Two papers in this volume (Otsu and Sumida, 1966; Rothschild, 1966a) can be used to obtain an estimate, though admittedly a shaky one, of the tuna catch of the Japanese longline fleet in the central Pacific. Otsu and Sumida have estimated the 1963 Japanese longline catch of tunas in the Pacific Ocean at 212,500 metric tons. From statistics published in the Japanese magazine Tuna Fishing, which is known to cover only a portion, though a large one, of the Japanese longline fishery, Rothschild has calculated that in 1963 the fleet expended about 31 percent of its Pacific effort in the central Pacific--much of it in an area within a radius of about 1,500 miles from Honolulu. If this percentage is applied to the total Pacific longline catch, one arrives at an estimate of 65,875 metric tons of tuna that the Japanese took in the central Pacific Ocean in 1963. In the same year, the feebly competitive Hawaiian

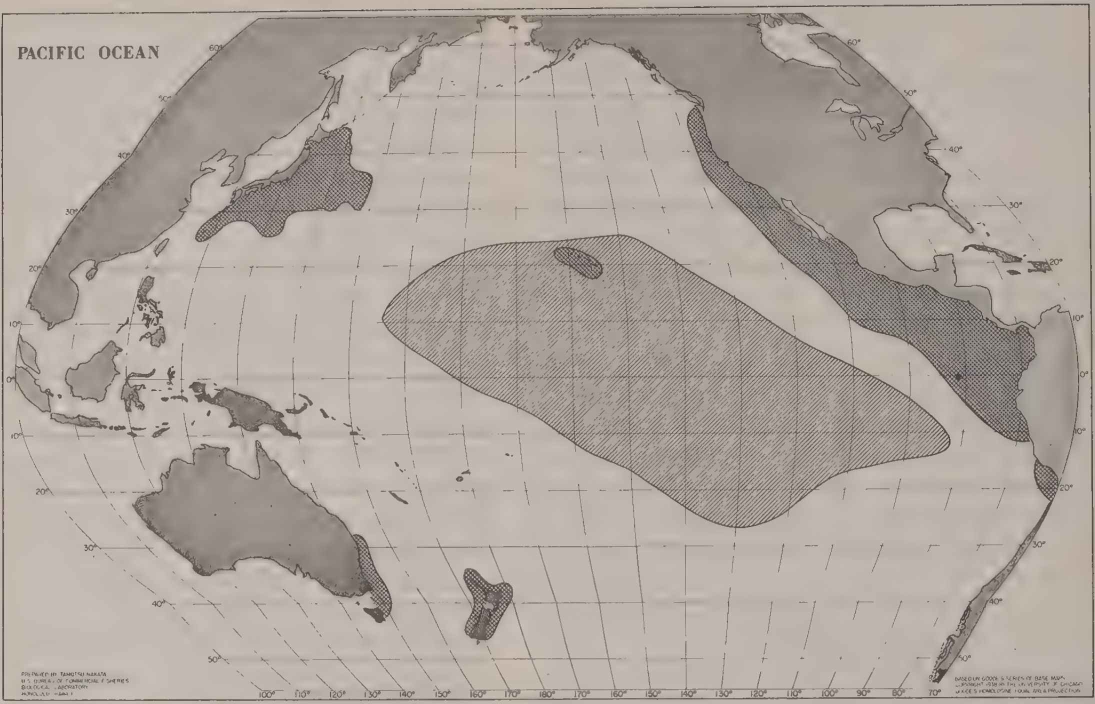
PACIFIC OCEAN
PREPARED BY TAMOTSU NAKATA
U.S. BUREAU OF COMMERCIAL FISHERIES
BIOLOGICAL LABORATORY
HONOLULU, HAWAII
BASED ON GOODE'S SERIES OF BASE MAPS
COPYRIGHT 1938 BY THE UNIVERSITY OF CHICAGO
GOODE'S HOMOLOSINE EQUAL AREA PROJECTION
100° 110° 120° 130° 140° 150° 160° 170° 180° 170° 160° 150° 140° 130° 120° 110° 100° 90° 80° 70°
60° 50° 40° 30° 20° 10° 0° 10° 20° 30° 40° 50°

Figure 1.--There are surface fisheries (marked here by cross-hatching) along the coasts of the Americas, off Japan, and around certain island groups in the Pacific. Deep-swimming tunas are taken predominantly by the Japanese longline fishery. The longline fleets range from Asia to the Americas. In 1963 about half their effort was concentrated in the area marked by hatching (Rothschild, 1966a).

longline fleet--took 674 tons of the same species (Lyles, 1966).

Thus one of the chief resources of the central Pacific is a very large stock of subsurface tunas that is being harvested, with an efficiency that is not known, by Japan. Fishermen agree that because of economic reasons the United States cannot compete directly, boat for boat, in the longline fishery (although, the Conference suggested, the Hawaiian longline fleet might increase its catch three or four times if more of the ships left the shelter of the islands and fished farther from home than the 90 miles that mark the range of most). But are there other resources, unavailable to the longline fleet, that are not now being fully utilized? It turns out that there is at least one, and that it is very large. Much of the work of the Conference went into defining that resource, estimating its yield, and calculating the chances of harvesting it.

That convenient statistical myth, the average American, ate 2.4 pounds of canned tuna in 1965 (Lyles, 1966). His taste for it has been whetted over the years: 20 years ago he ate only a quar-

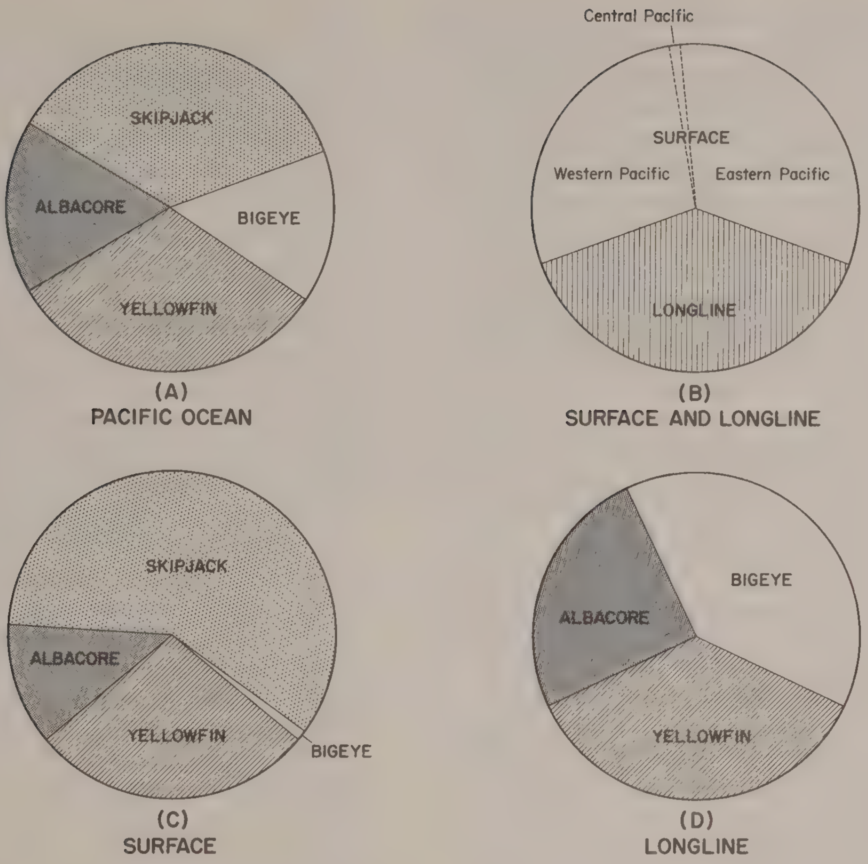

Figure 2.--(A) Four species dominate the catch of tunas in the Pacific Ocean. They are the albacore, the bigeye tuna, skipjack tuna, and yellowfin tuna. By weight, the skipjack tuna, taken almost always at the surface, makes the largest contribution. (B) In total landings, the surface fisheries provide 61 percent of the Pacific tuna catch. (C) The skipjack tuna constitutes the major species caught at the surface. (D) Bigeye and yellowfin tuna make almost equal contributions to the longline catch. (For sources of data, see table 1.)

ter as much. Other peoples like tuna, too. The Greeks were eating bluefin tuna over 2,000 years ago. The first known cookbook, that of Apicius (first century A.D.), tells how to cook tuna in imperial Roman style: Bake it and cover it with herbs, onions, vinegar, honey, and the ubiquitous Roman sauce ‘‘liquamen,’’ made of small fish steeped several months in brine (Flower and Rosenbaum, 1958).

Among the several species of tunas, the most plentiful, many people believe, is the skipjack tuna. Along the shores of the Americas, where they are taken by purse seines along with yellowfin tuna, they contribute an average of 68,000 metric tons (1 metric ton equals

2,205 pounds) annually, most of which is landed by U.S. vessels based in California (Inter-American Tropical Tuna Commission, 1966). On the opposite side of the Pacific, about 127,000 metric tons a year are taken by the Japanese pole-and-line fisheries (Food and Agriculture Organization of the United Nations, 1965) (figs. 1 and 2 and table 1). In Hawaii, skipjack tuna constitute the chief commercial catch, ranging from 3,337 to as much as 7,327 metric tons in recent years. These are surface fisheries; in addition, a few large and old skipjack tuna are occasionally taken by the longline fleet. The fish are plentiful on both sides of the ocean, and in the center, at the same season. All three surface fisheries--off Japan, in the central Pacific, off the Americas--attain their peak catches in summer.

Table 1.--Estimated annual catches of four major species of tunas in the Pacific Ocean[1] (in thousands of metric tons)

	Albacore	Bigeye tuna	Skipjack tuna	Yellowfin tuna	Total
Surface fisheries					
Western Pacific	19.5	1.5	126.6	5.3	152.9
Central Pacific	-	-	4.1	-	4.1
Eastern Pacific	20.7	-	67.8	89.8	178.3
	40.2	1.5	198.5	95.1	335.3
Longline fishery					
Pacific-wide	52.8	83.8	-	75.9	212.5
Total	93.0	85.3	198.5	171.0	547.8

The youngest skipjack tuna, the larvae that have just hatched and are able to swim only feebly, have been found all the way across the Pacific from Malaysia to Ecuador. Their abundance west of the international date line cannot be guessed, for the Japanese, who have taken the most samples there, have published little of their data. East of the date line, though, all the material at hand points toward great abundance in the central Pacific, scarcity in the eastern. Near the island of Oahu, for example, more than 20 skipjack tuna larvae were found in each of four plankton tows taken during a single month. Yet in the eastern Pacific, 20 larvae were collected only after 8 long years of sampling (Matsumoto, 1966). The presence of larvae spells recent spawning, of course. Thus it is known that in equatorial waters some skipjack tuna are spawning all year round. In slightly cooler climes, as off Oahu, spawning is most pronounced in the summer.

Until they begin to enter the commercial catch at a length of about 14 inches, skipjack tuna are hard to locate. They can dodge the plankton nets that bring in the larvae. Much of the little information we have comes from predators which they cannot dodge, that is, larger fishes, whose stomachs sometimes yield juvenile skipjack tuna. The information thus obtained suggests that, as with the larvae, juvenile skipjack tuna are more abundant in the central Pacific than in the eastern. It took 13 years of examination of the stomach contents of larger fishes in the eastern Pacific to accumulate 10 juvenile skipjack tuna. Dip netting in the equatorial Pacific has yielded as many as 34 at one time (Higgins, in press).

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[1] Totals for the surface fisheries of the western Pacific were arrived at by subtracting from the total catches reported by the Japanese to FAO for 1960-63 (FAO, 1965), their estimated worldwide longline catch of each species for these years (Otsu and Sumida, 1966). Average catches for 1960-64 are shown for the central Pacific (Silliman, 1966) and eastern Pacific (IATTC, 1966). Estimated catches from the Japanese longline fishery are averages for 1960-63 (Otsu and Sumida, 1966). The small contribution of the Hawaiian longline fishery (500 tons of bigeye tuna, 100 tons of yellowfin tuna) is a 1960-64 average.

Skipjack tuna are about 44.4 cm. (about 17 inches) long when they are a year old, 64.9 cm. (25 inches) at 2 years, and 72.0 cm. (28 inches) at 3 (Rothschild, in press; Shomura, 1966). They are presumed to live 4 or 5 years. Some old fish have been caught that were just under 3 feet long and weighed over 35 pounds. No one knows for sure at what age skipjack tuna reach sexual maturity and begin to spawn.

The bulk of the skipjack tuna now caught in the Pacific are young fish. Off Japan, the catch is concentrated on fish between 36 and 65 cm. (14 and 25 inches), that is, fish that weigh less than 14 pounds--usually far less (Higgins, 1966). These would be fish that for the most part are well under 2 years old. In the eastern Pacific catch, most range between 50 and 60 cm. (19 and 23 inches), or about 5 and 10 pounds. These fish, too, are less than 2 years old.

Only in the small Hawaiian catch do larger, older skipjack tuna show up in considerable quantities. Even during winter, many are caught that are more than 70 cm. (27 inches) long and weigh nearly 20 pounds, and these fish 2-1/2 years old or older dominate the peak catches of the summer. In July, 90 percent of the skipjack tuna caught in the islands may weigh more than 15 pounds.

Now this is rather curious. Why should Hawaii alone regularly take skipjack tuna that are of a size rarely caught elsewhere?

The two most important skipjack tuna ever caught in Hawaii were landed in June 1962 and August 1962. They were both big fellows. They were important because they bore plastic tags that had been affixed to them about 2 years before, off the coast of Baja California, by scientists from the Inter-American Tropical Tuna Commission. They confirmed the supposition that some portion of the large fish that characterize the Hawaiian catch must have spent a part of their lives 3,000 miles away near the shores of Mexico.

Although the technique is the best yet devised to trace the migrations of fish, tagging is expensive. The fish must be caught twice: first when they are tagged and second in a commercial fishery. Few of those tagged ever show up in the catch, and most of them are taken not far from the tagging area. Very few survive the emplacement of the tag, the local fishery, and the natural hazards of life in the sea to be caught far enough away to establish long-range migratory patterns.

But the fish carry an ''inborn'' tag that may eventually tell much about migrations. Like all other animals, they inherit from the parent stock some inalterable physical characteristics. One of these is the presence of certain proteins on the red blood cells. By typing the blood of fishes, as the blood of humans is typed, scientists can sometimes tell whether the fish have come from a stock that breeds with no other. These discrete units are called subpopulations. Much work is being done on the subpopulations of fishes, particularly the tunas, and among the tunas, the skipjack. Scientists are beginning to be able to distinguish between the subpopulations of skipjack tuna. They face the knotty problem of defining the spawning areas and times of each subpopulation and determining the mechanisms that have led to and still contribute to reproductive isolation of these non-interbreeding, self-sustaining fractions of the population. Around Hawaii there seem to be at least three subpopulations. Simply as a working hypothesis, these have been assumed to consist of a local subpopulation, spawned and living out their lives in Hawaiian waters; another, transient subpopulation that comes from that large stock which supplies the eastern Pacific fishery with young fish; and a third, which is rarely seen, which might consist of fish from Japanese waters.

Many of the enigmas of the skipjack tuna catch of the central and eastern Pacific can be explained by hypothesizing that the fish are spawned in the equatorial central Pacific (where, it will be remembered, larvae and juveniles are relatively abundant). Early in life, they move to the shores of the Americas (where, it will be remembered, only young fish are found). They remain there only briefly, perhaps a matter of months, and as they begin to approach sexual maturity return to the central Pacific--those that are not caught in the eastern Pacific purse seines, that is. This remaining portion must be very large, for fishery biologists agree that the heavy demands imposed upon the species by the eastern Pacific fishery have failed to dent the stock. This escapement stock, as it is sometimes called, probably makes its home in the equatorial central Pacific (Rothschild, 1965). Some of it enters the Hawaiian catch, but the bulk of it is not available to the commercial fleet.

How large is this stock? The Conference addressed itself to this matter. Two estimates were prepared (Rothschild, 1966b; Silliman, 1966). The authors are the first to disclaim that these estimates are in any sense definitive. Indeed, both estimates were revised between their presentation at the Conference and their publication in this volume. But uncertain as they are, they stand as the first attempts to say more of the central Pacific escapement stock of skipjack tuna than that it is ''large'' or ''substantial.'' It turns out that the gains from this stock may indeed be, as O. E. Sette says in the Report of the Working Group on Skipjack (page 24) ''spectacular.''

What these estimates say is that there lives in the warm seas south of Hawaii one of the major fishery resources of the world, one that without appreciable harm to the basic stock can supply a minimum of about 150,000 metric tons of tuna a year (perhaps, Rothschild suggests, much more). Since the entire tuna catch of the United States in 1964 was 139,500 metric tons (Food and Agriculture Organization of the United Nations, 1965), the estimates imply that the United States could double its tuna catch if it could harvest these fish.

Where are the fish?

How can they be caught?

However it looks to us, to the fish the ocean is far from a featureless waste. It has its own provinces that are as sharply defined as the mountains and deserts on land. It has taken almost a century of research to learn how to identify these permanent features of the ocean. But although much more remains to be done, scientists are beginning to relate them to the abundance and availability of commercial fishes. Even with the imperfect state of present knowledge, it would be unnecessary to lay out an elaborate grid and search the central Pacific, square by small square, for its stock of skipjack tuna. The region to explore may be vast, but the job can be done. And possibly the ships need not travel thousands of miles to locate the fish. The creatures may be only a few score feet away--beneath the surface. Our knowledge of the occurrence of catchable skipjack tuna depends almost exclusively upon the fact that they can be sighted at the surface of the ocean. But they may visit there almost incidentally, spending most of their lives in deeper waters. There is no way to observe this from a fishing vessel. The best present method of locating subsurface fishes is to search them out with inaudible beams of sound--sonar. A wonderfully complex new sonar has been installed on the research vessel Townsend Cromwell of the Laboratory in Honolulu. One of its principal purposes is to locate tunas underwater and to tell scientists how the fish live there--whether they school, and for how long and how tightly; how fast schools move; all the thousand and one bits of information necessary to picture life beneath the surface in detail. At the time the Conference was held, the sonar was still being constructed in California. It was installed in March and April and the first training cruises have been made (Yuen, in press). A new world is being opened up.

If the bulk of the central Pacific stock is subsurface, then a further problem presents itself: How are they to be caught? Pole-and-line fishing and longlining have evolved in response to different aspects of tuna behavior. They probably are not adequate for taking the central Pacific stock.

A new fishery will probably call for new gear, possibly great underwater trawls, and new methods, as D. L. Alverson points out in the Report of the Working Group on Gear Development (page 39). The new gear, the new methods, will need to be shaped to the individual physiology and behavior of the species sought. Data on these topics are being rapidly accumulated (Manar, 1966). More will be acquired by use of the new sonar.

This is the picture, then. There exists in the central Pacific a fishery resource of immensely large size. Several lines of research are being pursued to make that resource available to commerce.

It was interesting to sit in the meeting room of the Naniloa Hotel in Hilo and hear the scientists tell their findings. The audience consisted of men from the industry, of fishermen, of newspaper reporters, County and State officials. Few were under 40. It was interesting to hear Professor Crutchfield sensibly point out that even though the resource were located and methods of harvesting it devised, the men present in that room might very well never profit from it personally, for such enterprises take, first, time, and second, great amounts of risk capital. And it is a moot question if it would necessarily be a Hawaiian industry; that seems to be up to the Hawaiians (Crutchfield, 1966). Yet, as the session went on, one became convinced that yes, this was the way an industry could develop. One could almost see the thousands of people it would support, directly or indirectly: the fishermen; the processors; the ship's chandlers; the shipyard workers; the bankers who would finance the canneries and the ships; the men who would sell the fishermen their cars and TV's or teach their children. This is the payoff of research, of course: but the gap between the quiet manipulation of statistical formulae and the opening of new supermarkets to take care of the new subdivisions that result when a new industry is established sometimes seems unbridgeably great. At Hilo it did not.

Tired, talked out, the conferees ended their meeting after lunch on Saturday. Most of them flew back to Honolulu that afternoon. Emerging from the thin overcast over Hilo, one saw that there was still snow on the crests of Mauna Loa and Mauna Kea. What were the positive results of the Conference? Several matters of short-range importance had emerged that offered promise to the present Hawaiian fisheries: a strong feeling that it was time to test the new Norwegian purse seines in the Hawaiian skipjack tuna industry; a plan to conduct the first operations analysis of the industry; many practical details that could mean not necessarily a vast new industry but a refreshed and more prosperous existing one. But the most exciting development was the effort to delineate the dimensions of the vast new industry that might be based upon a resource whose very existence was unsuspected not too long ago (fig. 3).

The fishponds of Molokai came in sight. They were a reminder that this kind of thinking was nothing new under the sun; men have been trying to put the sea to work for them a good long time, and often successfully.

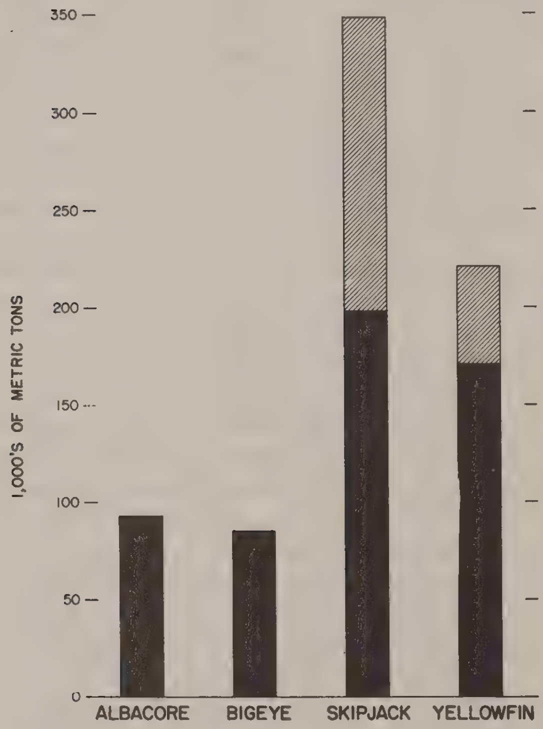

Figure 3.--The Governor's Conference estimated that the yellowfin tuna catch could be increased about 50,000 metric tons per year, the skipjack tuna catch 150,000 or more metric tons a year. These estimates (hatched) are here added to the average catch figures of table 1. The estimated skipjack tuna yield is greater than the present U.S. Pacific catch of all tunas.

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Skipjack Landings Could Be Doubled Scientists Disclose at Hawaii Meet

By Thomas A. Manar, Chief
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Since 1950, the California tuna fleet has only once taken less than 50.000 tons of Skipjack tuna per year in the fishery off the Americas, and has sometimes doubled that figure. Yet this steady drain on the resource has no measurable impact on the population.

Using fewer boats than ever before, the Hawaiian Skipjack tuna fishing fleet in 1965 racked up its highest catch in history (about 8,000 tons).

These two facts highlight a fishery mystery: fishermen and fishery scientists agree that the skipjack could well be the most plentiful of the tunas, but just how many of them are there in the Pacific Ocean?

This subject, and its implications, was the chief topic of discussion at a meeting of fishery experts in Honolulu and Hilo, Hawaii. The group met at the invitation of Governor John A. Burns of the State of Hawaii. Object of the Governor's Conference on Central Pacific Fishery Resources was to assess tuna stocks of the area and recommend methods of increasing the catch.

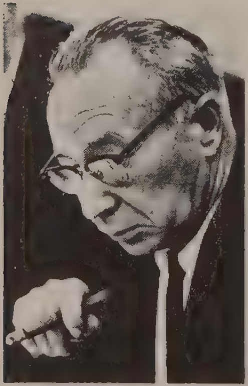
Divided into three sessions, the conference first saw a group of biologists weight the evidence on the abundance of skipjack, yellowfin, and bigeye tuna in the central Pacific. Next, the findings of the scientists were discussed with industry representatives and government officials. Finally, the group reported to the public on its findings.

Co-Chairmen of the conference were John C. Marr, director, US Department of the Interior's Bureau of Commercial Fisheries, Hawaii Area, and Michio Takata, director, Division of Fish and Game, Hawaii Department of Land and Natural Resources.

The participants agreed that the Skipjack tuna fisheries of the entire Pacific are too poorly documented to allow a reasonable estimate of the total ocean-wide yield. The most-studied of these fisheries, that in the eastern Pacific, however, permitted an estimate that suggests strikingly how vast the future harvest might be: the minimal estimate of yield for the stock in the eastern half of the central Pacific alone was about 150,000 metric tons a year, in addition to the 70,000 tons now being taken in the eastern Pacific off the Americas. In other words, if the United States could locate and catch the hidden Skipjack tuna, we could double or more than double our entire present tuna catch, which amounted to 139,500 metric tons in 1964.

These estimates ignore the Skipjack tuna that never appear in the eastern Pacific fisheries, such as fish less than one year old caught in Hawaii, off Japan, in the Trust Territory of the Pacific Islands, and in the South Pacific, where the fish are taken off South America, in French Oceania, and near Australia.

But locating and catching the Skipjack tuna of the central Pacific present formidable technical problems, the group emphasized. The fish are found over an area of 30 million



Albert L. Tester, University of Hawaii.

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—All Photos courtesy Honolulu Star Bulletin square miles, 10 times the size of the United States. Fishable schools of young Skipjack tuna appear along the margins of the Pacific, and fish of all age groups near Hawaii and in various Pacific island groups—beyond that, the life history of the species is little documented. What happens to the young fish that escape the nets of the eastern Pacific fishery is unknown, although there is good evidence(based on three tag recoveries) that some make their way across the Pacific to the longitude of Hawaii.

John C. Marr (left) and **Michio Takata**, co-chairmen, Governor's Conference on Central Pacific Fishery Resources, held in Honolulu early this summer. Photo by Honolulu Star-Bulletin.

Last year, Brian J. Rothschild of the BCF Laboratory in Honolulu published a paper in which he examined all available evidence on the Skipjack tuna and drew up a series of hypotheses to explain some enigmas of the catch ("Hypotheses on the origin of exploited Skipjack tuna *(Katsuwonus pelamis)* in the eastern and central Pacific Ocean," US Fish and Wildlife Service, Special Scientific Report — Fisheries 512, 20 p., 1965). This paper formed much of the basis of the discussion at the conference. Mr. Rothchild hypothesized that a substantial portion of the Skipjack tuna are spawned in the central Pacific and migrate to the eastern shores of the ocean, where they are fished by the California fleet. They remain there only a few months, and then return to the central Pacific to spawn.

Addressing itself to the problems of the Hawaiian fishery, the conference expressed interest in eliminating the use of live bait in the Skipjack tuna fleet. It recommended that some form of purse seining again be tried in Hawaiian waters. Experiments in 1950 and 1951 suggested that the method in use at that time could not be profitably adapted to the Hawaiian Skipjack tuna fishery, but recent improvements in the area of purse seining have made it appear worthwhile to try to net the fish rather than catch them on pole and line. There was much interest in the use of a lightweight seine similar to that used in the Norwegian Bluefin tuna fishery.

The conference pointed out, however, that although seining might improve the insular fisheries, such as that around Hawaii and those in the Trust Territory of the Pacific Islands, it would do little toward opening up the very much greater subsurface tuna resources in non-insular areas.

In that field, new methods of capture are likely to depend on the results of studies now under way at the BFC Laboratory in Honolulu. These deal with: the abilities of tunas to see, smell, and hear; their behavior; and their vertical distribution and degree of schooling. A continuous- transmission, frequency-modulated sonar on the research vessel *Townsend Cromwell*, installed in April 1966, is expected to provide fresh and vital information on vertical distribution and schooling.

Along with studies aimed at new methods of capture must go further work in locating areas of abundance, the conferees said: "These could be sought out . . . by laying out an observational grid or pattern and making a sonar survey of tuna abundance over such a pattern. If nothing were known about the biology and oceanography of the tropical Pacific, this would be the best way to proceed. However, enough is known so that the observational pattern could be oriented around areas which various lines of evidence suggest may be areas of tuna abundance. Concentrations of tuna larvae indicate the presence of concentrations of spawning adults. The association of Skipjack with the broad boundary of California Current extension as it moves seasonally through the Hawaiian Islands suggest the association of Skipjack with the boundary when it is south of the Hawaiian Islands, or perhaps with similar boundaries elsewhere. Other features of circulation and water conditions which lead to concentrations of tuna should be sought.

"Again, when non-insular areas of tuna abundance are found, given appropriate gear, there is the problem of providing the economic feasibility of a fishery based on that area.

Although strongly emphasizing the potential of the Skipjack tuna fishery, the conference also considered the possibilities of two other fisheries, those for Yellowfin and Bigeye tuna. Estimates of potential catch of Yellowfin tuna were placed at an increase of 30,000 to 50,000 metric tons over the present Pacific longline catch of 100,000 tons by the Japanese (the eastern Pacific fishery was excluded from consideration). Little increase in Bigeye tuna catch of 100,000 tons on longlines was seen as possible.

Cited as one of the chief scientific problems facing tuna research was that of establishing the identity of subpopulations of the various species. The BCF Laboratory in Honolulu has developed techniques to distinguish between subpopulations of Skipjack tuna. To date at least two such subpopulations have been identified in the Hawaiian fishery, one of which is indistinguishable from a subpopulation in the eastern Pacific fishery.

SALMON OF THE NORTH PACIFIC OCEAN—PART VI

SOCKEYE SALMON IN OFFSHORE WATERS

by

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INTRODUCTION

In Part I of *Salmon of the North Pacific Ocean*, a portion of which constitutes the introduction to subsequent parts, Jackson (1963) explained the organization and purpose of the comprehensive report as a whole and the general contents of its individual parts. In the present contribution (Part VI), the oceanic distribution, migrations and extent of intermingling of the various stocks of sockeye salmon (*Oncorhynchus nerka*) will be described, mainly from data obtained from 1955 to 1962, inclusive. The studies which yielded this information will be reviewed and assessed, followed by a general summation of the available knowledge.

Information on high seas distribution of specific stocks or groups of stocks has been obtained from tagging, parasitological and morphological studies, and studies of scale characteristics. Extensive serological research has been conducted but results applicable to recognizing the oceanic distribution of the principal sockeye stocks have not been obtained. Nevertheless, these serological studies will be reviewed to indicate their scope and their potential value.

As background information for the main purpose of this paper, a brief account of the life history, distribution of spawning stocks and the general high seas distribution of sockeye will be provided.

LIFE HISTORY

The sockeye salmon typically spawns in the summer or autumn in streams tributary to lakes, in outlets of lakes, or in lakes themselves, which are accessible to the sea. Much less frequently, spawning occurs in streams which are not associated with lakes and, as is the case with some Kamchatkan (U.S.S.R.) stocks, in springs. Apparently, all major populations of sockeye spawn in areas where the newly-hatched young have ready access to a lake.

The eggs are deposited in gravel beds where they are incubated throughout the winter. Hatching occurs in late winter, spring or early summer, the alevins remaining in the gravel until the yolk sac is absorbed or even longer. The fry emerge from the gravel one to two months after hatching and swim upstream or downstream, as necessary, to reach the lake nursery area. The fry of sockeye which spawn in springs utilize the springs as growing areas. The fry of sockeye which spawn in streams not associated with lakes migrate directly to sea.

In the lake, after a short period of residence along the shores, the fry take up a pelagic life, feeding mainly on zooplankton. In springs, the food consists mainly of benthonic organisms including crustacea, larval and pupal insects, and oligochaetes. The length of freshwater residence, excluding those fish which go to sea as fry, is usually one or two years, less commonly three years and rarely four years. Seaward migration occurs in the spring months of their second to fifth year of life.

In the ocean the sockeye maintains its pelagic way of life and feeds on zooplankton, squid and small fish. After a growth period of usually 2+ or 3+ years the adult sockeye returns to its natal waters to spawn. Some sockeye, especially males, return to spawn after 1+ years at sea and some remain in the sea as long as 4+ years. Spawning sockeye are most commonly in their fourth to sixth year of life, but the entire range appears to include the third to eighth years. Ages of spawning sockeye have been reported as 3_1, 3_2, 4_1, 4_2, 4_3, 5_1, 5_2, 5_3, 5_4, 6_2, 6_3, 6_4, 7_3, 7_4, 7_5, 8_4 and 8_5, with ages 4_2, 5_2, 5_3 and 6_3 being the most important[1]. In a few stocks, ages 6_2, 6_4 and 7_4 may form substantial portions of the spawning fish.

The maturing sockeye returning from the sea enter their rivers of origin from May to October. A variable period of time, up to two months, may be spent in fresh water (mainly in lakes) prior to spawning. Death follows shortly after spawning.

Such features in the life history as the age at seaward migration and the time of migration, the length of ocean residence, the total age at time of spawning and the time that maturing fish enter the rivers, vary widely among the many sockeye stocks. The timing of the seaward migration of smolts, of the upstream migration of adults, and of spawning remains relatively constant from year to year for individual stocks. Each stock also has its own characteristic age categories, although the relative proportions of the individual age categories may vary considerably from year to year.

For greater detail of the sockeye's life history, reference is made to Part III of *Salmon of the North Pacific Ocean;* Hanamura (1966) described the life history of Asian sockeye stocks and Ricker (1966) described that of British Columbia (Canadian) stocks.

INSHORE DISTRIBUTION AND TIMING OF UPSTREAM MIGRATION

Sockeye salmon reproduce in Asian watersheds from the northern Kuril Islands in the south to the northern Bering Sea coast of the U.S.S.R., and in North American watersheds from the Columbia

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[1] In this system of designating ages of sockeye salmon, the first number represents the year of life of the fish, counting from the time of egg deposition, and the subscript represents the year of life in which the fish went to sea.

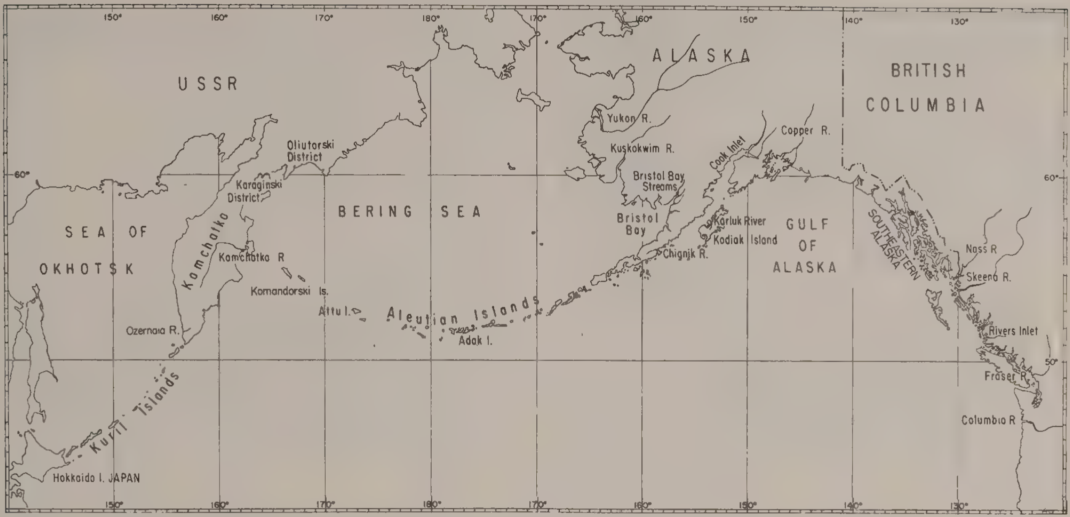

150°
160°
170°
180°
170°
160°
150°
140°
130°
60°
50°
U S S R
SEA OF OKHOTSK
Oliutorski District
Karaginski District
Kamchatka
Kamchatka R
Komandorski Is.
Attu I.
Aleutian Islands
Adak I.
Ozernaia R.
Kuril Islands
Hokkaido I. JAPAN
BERING SEA
ALASKA
Yukon R.
Kuskokwim R.
Bristol Bay Streams
Bristol Bay
Cook Inlet
Copper R.
Karluk River
Kodiak Island
Chignik R.
GULF OF ALASKA
BRITISH COLUMBIA
SOUTHEASTERN ALASKA
Nass R
Skeena R.
Rivers Inlet
Fraser R.
Columbia R

FIGURE 1. Map of North Pacific region encompassing the areas of sockeye salmon distribution.

River (U.S.A.) in the south to the northern Bering Sea coast of Alaska. However, the larger, commercially important stocks of sockeye have a much more limited range.

The principal sockeye stocks in Asia are confined to river systems of the Kamchatka Peninsula. According to Krogius and Krokhin (1956) the stocks from the Ozernaia River on the southwest coast of Kamchatka and those from the Kamchatka River on the central east coast of Kamchatka (Fig. 1) account for about 90% of the commercial sockeye catch in Asian waters. River systems contributing to the remainder of the catch occur on both the west and east coasts (including the Oliutorski and Karaginski districts) of Kamchatka and, to a lesser extent, on the northern Okhotsk Sea coast. Catch statistics for Asian sockeye fisheries may be found in Kasahara (1963) and Taguchi (1956, 1957).

In North America the most important sockeye stocks occur in the rivers tributary to Bristol Bay (western Alaska) and in the Fraser River system (British Columbia). (The five principal sockeye-producing river systems in Bristol Bay are the Kvichak, Naknek, Nushagak (Wood), Ugashik and Egegik.) Other regions of sockeye production of considerable commercial importance occur in central Alaska (Cook Inlet, and Chignik, Karluk and Copper rivers), British Columbia (Rivers Inlet, Skeena and Nass rivers) and, to a lesser extent, southeastern Alaska. Catch statistics of fisheries in various North American areas are reviewed by Kasahara (1963), as well as in INPFC (1962a, pp. 1–67 ; 1962b, pp. 1–51 and 61–66). A general impression of the relative abundance of sockeye along different parts of the coast may be gained from examination of Table 1, which summarizes North American sockeye catch data for a number of years.

TABLE 1. Average annual catches of sockeye salmon in various North American regions, in millions of fish[1].

Years	Western Alaska	Central Alaska	South-eastern Alaska	British Columbia	Washington[2]
1921–1930	15.0	5.8	1.9	4.0	1.3
1931–1940	17.4	7.0	1.9	4.2	1.3
1941–1950	10.9	5.6	1.1	4.2	1.5
1951–1960	7.3	3.0	0.9	4.9	2.2

[1] From Table 71 of Kasahara (1963), correcting western Alaska in 1926 to 20.1 million instead of 10.1 million.

[2] Mostly Fraser River fish.

It is generally recognized (Kasahara, 1961, p. 25) that the combined size of North American sockeye stocks is greater than that of Asian stocks. However, a close comparison of the magnitudes of the sockeye stocks of both continents is not possible. To make such a comparison of total stock sizes it would be necessary to know not only the commercial catch but also the escapement to the spawning grounds of the various river systems. Since the escapement is known for only some stocks and some years, it becomes necessary to rely primarily on catch data to provide an indication of relative stock size. It must be emphasized, however, that the proportion of the total run represented by the catch varies among fishing areas and among years. For example, in the years 1946 to 1952, inclusive, the catch varied annually from approximately 44% to 72% of the total runs to Bristol Bay rivers (see Tables 51 and 77 in Kasahara, 1963); from 1940 to 1952 it varied from approximately 33% to 89% of the total runs to the Ozernaia River (see Table 6 in Egorova *et al.*, 1961); and from 1951 to 1961 it varied from approximately 65% to 85% of the total runs to the Fraser River (see Table 64 in Kasahara, 1963). In Table 2, data on North American and Asian catches are given for the years 1927–30, 1933–36, and 1940–52. Catch data for earlier years are incomplete for Asia (see Table 43, Kasahara, 1963) and in the years from 1953 onward a high seas fishery has existed in waters westward of 175°W for which the catch, on the basis of available data, cannot be accurately assigned to rivers or even continent of origin. As noted later, this high seas fishery is prosecuted in oceanic regions where, and at times when, the sockeye are largely, if not entirely, of Kamchatkan or western Alaskan origin.

TABLE 2. Catch of sockeye salmon in Asian and North American waters, in millions of fish.

Year	Asia[1]	North America[2]	Total
1927	9.8	22.9	32.7
1928	15.4	30.6	46.0
1929	11.2	24.5	35.7
1930	12.7	20.2	32.9
1933	8.8	36.8	45.6
1934	20.0	40.7	60.7
1935	8.2	15.8	24.0
1936	14.9	41.1	56.0
1940	10.3	17.2	27.5
1941	11.7	22.9	34.6
1942	10.1	24.0	34.1
1943	9.5	28.8	38.3
1944	6.3	22.6	28.9
1945	4.7	19.7	24.4
1946	4.9	25.2	30.1
1947	3.8	30.2	34.0
1948	2.3	23.6	25.9
1949	3.3	16.1	19.4
1950	3.4	19.7	23.1
1951	2.9	15.2	18.1
1952	4.1	23.1	27.2
21-year mean	*8.5*	*24.8*	*33.3*

[1] From Table 43 of Kasahara (1963).

[2] From Table 71 of Kasahara (1963).

For the 21 years shown in Table 2, the North American sockeye catch varied annually from 61.4% to 91.1% of the total catch, with a mean of 75.6%.

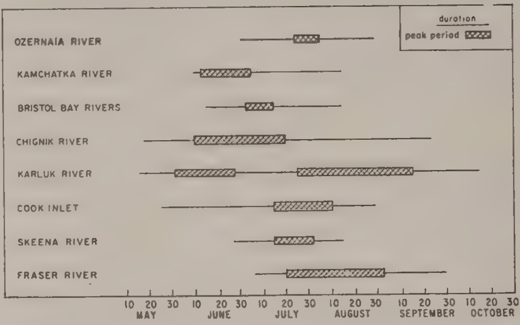


FIGURE 2. Approximate timing and duration of sockeye salmon migrations into their rivers of origin. (Based on data provided at the Seventh Annual Meeting of INPFC, Vancouver, B.C., 1960; by Japan for Asian rivers, and by Canada and the United States for North American rivers.)

As noted previously, the period of upstream migration of adult sockeye varies among stocks but is relatively constant from year to year for individual stocks. Figure 2 shows the times of arrival of the principal sockeye stocks in fisheries at or near the mouths of their rivers of origin. It is clear that there are marked differences in the time and duration of peak migration among some of these major stocks. For example, in Asia the peak period of upstream migration of Kamchatka River sockeye ends about three weeks before the start of the main upstream migration of Ozernaia River sockeye; in North America the bulk of the Fraser River sockeye does not start moving upstream until about one week after the end of the peak migration period in Bristol Bay rivers.

The peak period of upstream migration indicated in Figure 2 for Fraser River sockeye perhaps warrants further explanation. The sockeye of the Fraser River are composed of several major stocks (as well as a number of minor stocks) associated with individual tributaries of the Fraser River. The stocks in each of these tributaries have their own characteristic peak migration period. The range of the peak period shown in Figure 2 is a composite of the peak periods of the individual major stocks.

GENERAL OFFSHORE DISTRIBUTION

The analysis of high seas salmon catch data obtained from Canadian, Japanese and United States research vessel fishing operations during the years 1955–60, and from the Japanese mothership fishery during the years 1952–60, has been presented in Part V of *Salmon of the North Pacific Ocean* (Manzer *et al.*, 1965). These authors stated that, although the catches revealed annual variations in abundance levels and relative proportions of immature and maturing individuals, a basic general distribution pattern prevailed. The following selected quotations from Manzer *et al.* (1965, pp. 52–57) describe the general features of this distribution pattern on a monthly basis from May through August. Figures 3 and 4 show schematically the distribution, relative abundance and proportions of maturing and immature sockeye salmon in the North Pacific Ocean and Bering Sea.

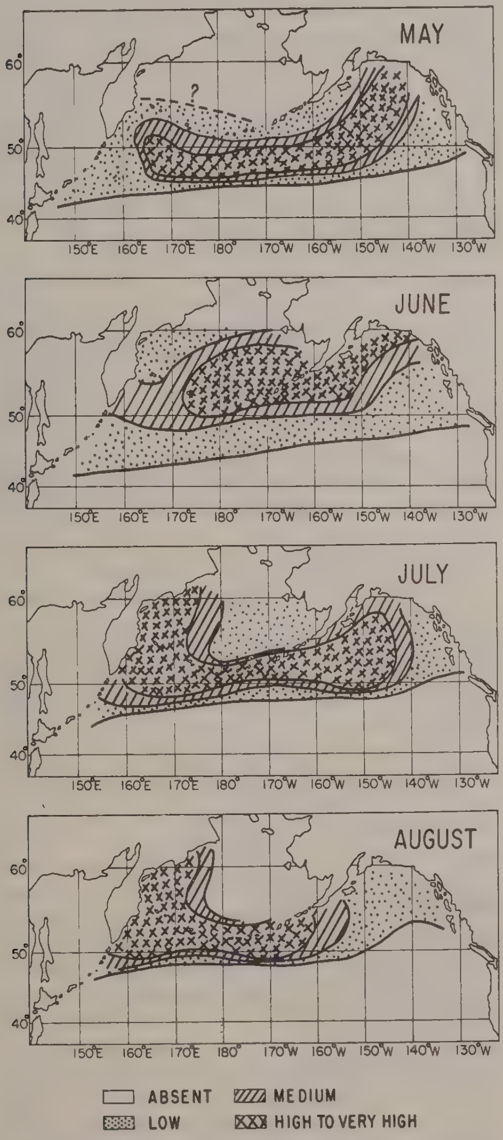

MAY
JUNE
JULY
AUGUST
?
60°
50°
40°
150°E 160°E 170°E 180° 170°W 160°W 150°W 140°W 130°W
ABSENT
MEDIUM
LOW
HIGH TO VERY HIGH

FIGURE 3. Schematic diagram showing distribution and relative abundance of sockeye salmon, May through August, maturing and immature fish combined (Figure 12 of Manzer *et al.*, 1965).

In *May*, sockeye salmon occur widely in the North Pacific north of a line which, in the western Pacific is located between Latitudes 42°N and 45°N and, in the eastern Pacific, between Latitudes 47°N and 49°N. Within this territory, sockeye are

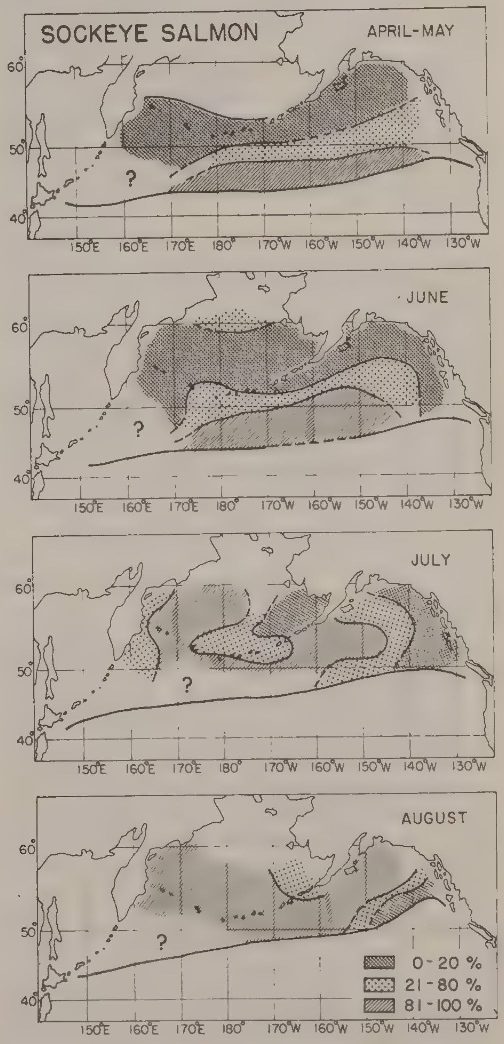

SOCKEYE SALMON
APRIL-MAY
JUNE
JULY
AUGUST
?
60°
50°
40°
150°E 160°E 170°E 180° 170°W 160°W 150°W 140°W 130°W
0 - 20 %
21 - 80 %
81 - 100 %

FIGURE 4. Schematic diagram showing the relative proportions of immature and maturing sockeye salmon in the North Pacific and Bering Sea, by month. Legend shows percentages of immature fish. (Figure 14 of Manzer *et al.*, 1965.)

most concentrated offshore from southwest and south of the Aleutian Islands eastward to south of the Alaska Peninsula and northeastward into the Gulf of Alaska. Their numbers decline in all directions from this large region. Although sockeye are known to occur in the southern Bering Sea in May in some years, the extent or annual consistency of their occurrence in the Bering Sea is not known. Also, it is not known whether they occur in the Okhotsk Sea.

In the southern latitudes, virtually the entire high seas population in May consists of immatures. Northward and coastward from this area their importance in the population decreases. In the western Pacific immediately south of the Aleutian Islands and in the northern Gulf of Alaska, the sockeye populations consist almost exclusively of maturing individuals.

In *June*, sockeye are more widespread than in May, occurring throughout the Bering Sea and at least southwest of Kamchatka in the Okhotsk Sea, as well as in the North Pacific. Some spatial changes in the relative importance of maturing fish and fish of different ages can also be noted, particularly during the latter part of the month.

In the northwest Pacific, abundance levels are about the same as in May, but older, maturing sockeye gradually are replaced by younger, immature individuals. . . . South of the Aleutian Islands and the Alaska Peninsula, sockeye are relatively more abundant than in May and the area of concentration has shifted northward. . . . Immatures are dominant by the end of the month. In the Gulf of Alaska relative numbers decline from the northwest to southeast. Maturing, 3-winter-ocean fish are mainly present in northern waters. Offshore and southward, younger, immature fish are more numerous and are dominant in the southwest areas of the Gulf.

In the Bering Sea, sockeye are concentrated in the southern central and eastern areas in June, thus extending the dense concentration of sockeye salmon located south of the Aleutian Islands. . . . [Sockeye are much less abundant in the western Bering Sea.]

In the Okhotsk Sea, sockeye are not particularly abundant in June. Fish here are virtually all maturing and include many age types. . . .

During *July*, marked changes occur in the distribution, ages and maturity of sockeye salmon, as maturing individuals evacuate the high seas areas, thus leaving a large residue of immature fish in all areas except those adjacent to coastal spawning areas off the east coast of Kamchatka and North America. Abundance levels in the northwest Pacific increase progressively through the month to relatively high levels. . . Abundance levels also continue to be relatively high south of the Aleutian Islands and into the western Gulf of Alaska. In these waters, however, sockeye are immature. . . Further shoreward [in the Gulf of Alaska], abundance levels decline and . . . maturing fish dominate the catches.

In the Bering Sea in July, abundance levels are highest in the western areas and decline rapidly eastward. Whereas sockeye were very abundant in the eastern Bering Sea in June, they are now virtually absent. Except for those in areas immediately offshore, the fish are virtually all immature and consist of sockeye which have spent either one or two winters at sea.

In the Okhotsk Sea, sockeye are more abundant in July than in June, reflecting immigration to the area. They are, however. much less numerous than in the western Pacific. . . . Immatures, while present, do not constitute an important element of the sockeye present.

During *August*, further changes occur in the distribution of sockeye salmon. The southern limit has shifted northward since May in association with warming of the surface waters from the south, . . Sockeye salmon occur almost as far south as Latitude 48°N in the western Pacific and, in the eastern Pacific, as far south as about Latitude 52°N. In the northwest Pacific off Kamchatka, there are fewer sockeye in August than in July, but they are still nevertheless relatively numerous and consist almost entirely of immature fish. South of the Aleutian Islands, immatures are still very abundant. . . South of the Alaska Peninsula and in the western Gulf of Alaska, immatures . . . constitute the sockeye population in August, but their numbers are lower than in July. Further east, in the central and coastal Gulf of Alaska, sockeye are scarce. Only in the southeastern sector do maturing fish dominate in the catches.

In the Bering Sea, the distribution pattern in August is much like that in July.

Since the preparation of the report by Manzer *et al.* (1965), fishing by research vessels has taken place in the winter and early spring. The results of the winter surveys (French, 1964, 1966; French and Mason, 1964) have shown that within the area of operations sockeye were distributed in the North Pacific from 175°E to 135°W in the months from January to March. The southern limit within this area was demonstrated to be at about 45°N. The waters west of 175°E in the North Pacific have not yet been fished in the winter. The winter distribution of sockeye extends into the Bering Sea, where they have been found northward to between 57°N and 58°N in the west-central region. Fishing in April (INPFC, 1964a, pp. 30–42; 1964b, pp. 42–46) has revealed large concentrations of sockeye in the central Gulf of Alaska.

INFORMATION ON DIRECTION OF MOVEMENTS AND RATES OF MIGRATION

Direction of Movements

Information on the direction of movement of sockeye salmon on the high seas has been obtained primarily from two sources—purse seine operations by United States tagging vessels and recoveries of tagged fish. In addition, the United States has carried out some experiments to study direction of movement using surface gillnets.

Purse Seine Operations

The directional aspect of purse seine tow hauls has been described in detail by Hartt (1962, 1966). Briefly, the seine was held open at an approximate angle of 120°, and in a given direction, for a standard period of time, roughly 30 minutes. Generally speaking, consistently good catches were taken to indicate that fish were moving primarily in the opposite direction to which the seine was being held open. During 1956–58 (Hartt, 1962) a small number of " opposing " sets was made, that is, a second set made immediately following the completion of the first, with the net held open in the opposite direction to the first set. Many more such " opposed " sets were made during the 1959–60 seining operations (Hartt, 1966). The results summarized below are based on the operations of five years, as described in the two reports cited above.

The seining operations demonstrated a pronounced westward movement of sockeye salmon south of the Aleutian Islands that was evident from Attu Island to the Alaska Peninsula. At times eastward movements were also observed, but these were of relatively minor importance. It was also shown that the greatest concentrations of sockeye occurred within about 15 miles of shore. Maturing sockeye salmon predominated in this westward flow until mid to late June and were progressively replaced by large concentrations of immature fish.

Seining in the Aleutian passes identified northward movements of large numbers of both maturing and immature sockeye into the Bering Sea. Several passes were shown to be of particular importance, either to the maturing or immature fish, or to both.

Partly due to lack of sufficient seining effort, direction of movement of sockeye salmon in the Bering Sea was much less well demonstrated than it was south of the Aleutians. However, a pronounced eastward movement of maturing sockeye salmon was evident from seine catches made in the eastern half of the Bering Sea, at least from 180° eastward. Some westward as well as eastward movement was indicated at times in the central and western Bering Sea.

Purse seining in the central Gulf of Alaska has provided little positive information on the direction of movement of sockeye salmon in those waters. Catches were usually small and similar regardless of the direction in which the seine was set. Probably movement there is more random in relation to feeding activity. However, longlining and tagging operations (see later section) have shown that maturing sockeye salmon of stocks extending from Bristol Bay to the Columbia River may be present in this area during the spring and early summer, and that they migrate out of the area in various directions to return to their final destinations.

Gillnetting Operations

In 1959 and 1960 the United States carried out experiments in the Aleutian area to study the direction of movement of salmon on the high seas by the use of surface gillnets. The results have been described by Johnsen (1964).

The method involved setting the nets in a particular direction, and relating the catch to the direction of entry of the fish and to the average lay of the set (that is, the average of the direction of the nets when set in the evening and when hauled in the morning).

The method is not considered to be sufficiently precise to describe accurately the direction of movement of salmon in the area, and many of the results are questionable. However, in a general way the results for sockeye salmon conform to those determined by the purse seine operations—that is, they indicate a strong westward movement of salmon along the south shore of the Aleutians, northward movements through the Aleutian passes, and eastward and westward movements within the Bering Sea.

Tagging Operations

Although the true direction of movement of salmon at sea cannot be determined merely by directly relating tagging and recovery locations, series or patterns of recoveries can provide reliable indications of the general direction of movement. Much detailed information has been collected on this aspect of the ocean distribution of sockeye salmon, which can be summarized here only briefly. To this end reference is made to Figures 31–42 and 45–53, and to the diagrams and data contained in Hartt (1962, 1966) and INPFC (1956 to 1961, 1963, 1964 a, b).

These data indicate that maturing western Alaskan sockeye approach the Aleutian Islands over a broad front from the south, east and west, at least in some years from as far west as 167°E and from as far east as 142°30′W. The source of the main concentration is probably from south of the eastern Aleutian area extending into the Gulf of Alaska.

Those fish which have travelled north or west to reach the land masses of the Alaska Peninsula and the Aleutian Islands continue westward and enter the Bering Sea through the Aleutian passes; others, those that are already farther to the west, may enter the Bering Sea more directly, moving either northward or north and east. The extent of westward movement is variable but appears to be related to the point at which they first reached the land—that is, in the main they probably make use of the first major pass to the west. The principal routes into the Bering Sea may also vary from year to year (see Fig. 26 of Hartt, 1962).

Once in the Bering Sea there is a general movement more or less directly towards Bristol Bay, but it is also evident that some considerable dispersal northwards may first occur. It should also be noted that recent evidence from United States gillnetting operations has indicated that some sockeye, at present of undetermined origin, may even winter in the Bering Sea (see French and Mason, 1964).

The principal source of the sockeye returning to east and west Kamchatka appears to be more westerly than that of western Alaskan sockeye, and primarily from well to the southeast of the Kamchatka Peninsula. However, tagging results have also shown a source from the westward " stream " migrating along the south shores of the Aleutian Chain.

Canadian longlining and tagging operations in the Gulf of Alaska in 1962 have given some general indications of the direction of movement of maturing sockeye of several stocks whose presence there during the spring and early summer has been identified (INPFC, 1964 a).

Maturing sockeye salmon originating from Bristol Bay southwards to the Columbia River were found intermingled in the offshore waters of the Gulf. Bristol Bay sockeye tended to be distributed in a northeast-southwest direction, and appeared to leave the Gulf early in the season (there being no recoveries later than from mid-June taggings) in a northwesterly direction. Maturing Kodiak Island sockeye also tended to be distributed over a northeast-southwest front, and to have moved towards Kodiak in a northwesterly direction. However, their presence in the Gulf in 1962 extended until relatively late in the season, into the July 3-July 14 tagging period at least. Sockeye originating in the northern areas of the Gulf (Cook Inlet to Copper River) shifted northwards and left the Gulf mainly earlier in the season than more southern stocks. Stocks originating from southeastern Alaska to the Fraser River were dispersed over a broad east-west front, and appeared to have moved first northwards, then eastwards towards the coast during the course of the season (mid-April to late July).

RATES OF MIGRATION

Maturing Western Alaskan Sockeye

Hartt (1962, 1966) provided relevant data and discussed the rate of travel of maturing western Alaskan sockeye. From taggings conducted during 1956–58 (Hartt, 1962), and based on recoveries in Bristol Bay from fish tagged in the far western Aleutian area, or from north of the Aleutians, including

TABLE 3. Rates of migration (nautical miles) of maturing western Alaskan sockeye salmon tagged by the United States in the Aleutian area in 1960[1].

		High seas returns[2]					Bristol Bay coastal fishery returns				
Area of release	Date of release	No. of returns	Average no. of days out	Average no. of miles traveled	Average no. of miles per day (unadjusted)	Average no. of miles per day (allowing one day delay)	No. of returns	Average no. of days out	Average no. of miles traveled	Average no. of miles per day (unadjusted)	Average no. of miles per day (allowing one day delay)
E7550	5/18–31	7	17.0	300	17.6	18.7	8	42.0	1,000	23.8	24.4
8052	6/16	9	4.6	85	18.5	23.6	8	30.5	820	26.8	27.8
8050	6/1	3	12.0	9	7.5	8.2	2	40.0	945	23.6	24.2
"	6/6	20	11.2	200	17.8	19.6	10	37.0	975	26.4	27.0
"	6/7	5	11.4	265	23.2	25.5	3	37.3	975	26.2	26.8
"	6/10	19	7.8	165	21.2	24.3	9	33.4	915	27.4	28.2
W7552	6/21	—	—	—	—	—	65	22.8	595	26.1	27.2
W7550	6/7	11	12.1	250	20.7	22.5	8	34.1	870	25.5	26.2
W7054	6/20	—	—	—	—	—	7	18.6	465	24.6	26.4
W7052	6/9	—	—	—	—	—	40	26.2	690	26.2	27.3
"	6/10	—	—	—	—	—	67	25.3	685	27.1	28.2
"	6/11	—	—	—	—	—	65	24.5	690	28.1	29.3
"	6/16	—	—	—	—	—	39	25.3	685	27.1	28.2
"	6/17	—	—	—	—	—	92	23.6	685	29.0	30.3
"	6/28–7/2	—	—	—	—	—	6	19.4	640	32.9	34.8
Totals and weighted means		74	10.2	194	19.0	21.2	429	25.5	695	27.2	28.4

[1] Reproduced from Table 6 of Hartt (1966).

[2] Includes only high seas returns that were apparently en route to Bristol Bay. Days out for high seas returns have been corrected for the one day difference due to the Japanese using the date west of the International Date Line.

several tagged near the Pribilof Islands, he concluded that during their last 40 days at sea " a fair average rate of travel for maturing red salmon " was probably 30 miles a day. (All rates given here are in terms of nautical miles.)

In dealing with rates of travel of maturing sockeye salmon based on data obtained from the United States tagging operations during 1959–60, Hartt (1966) selected a number of the more reliable recoveries and summarized them in his Table 6, which is reproduced here as Table 3. These data include recoveries made on the high seas of fish presumably en route to Bristol Bay, as well as recoveries made in the Bristol Bay coastal fisheries. From these data it was determined that the rate of travel of maturing sockeye tagged directly south of the Aleutians and recovered in the Japanese mothership fishery averaged 19.0 miles a day, or 21.2 miles a day after allowing for one day's delay as a result of being tagged (for reasons which he describes in some detail). The recoveries made in the Bristol Bay coastal fisheries averaged 27.2 miles a day unadjusted, or 28.4 miles a day after again allowing for one day's delay due to tagging effects.

Thus Hartt concluded that the fish that were recovered nearer to where they were tagged (that is, the high seas recoveries) travelled at a slower rate than those that were recovered in Bristol Bay—19.0 miles a day as compared with 25.8 miles a day for the same experiments.

From the data presented in Table 3, Hartt also pointed out that an apparent change in rate of travel occurred during the course of the migration season, with fish tagged later exhibiting an apparently faster rate of travel than those tagged earlier. In his area W7052, for example (Table 3), where tagging was conducted from June 9 to July 12, the rate of travel increased from 27.3 miles a day on June 9 to 34.8 miles a day for the period June 28 to July 2 (both rates being adjusted for delay due to tagging). In considering these differences it must of course be recognized, as Hartt points out, that it is not known whether there was actually a true difference in rate of travel, or whether the difference was rather due to differences between the groups in the directness of the routes by which they travelled to Bristol Bay.

Maturing Kamchatkan Sockeye

Mr. H. Kondo of the Hokkaido Regional Fisheries Research Laboratory (personal communication) has provided data on the rates of migration of maturing Kamchatkan sockeye which are summarized in Table 4. These recoveries were selected from many high seas recoveries of maturing sockeye tagged by Japan on the following basis: they included only those that were tagged west of 175°E (to ensure high probability

TABLE 4. Rates of migration of maturing Kamchatkan sockeye salmon tagged by Japan off southeast Kamchatka, 1958–61[1].

Date of release	Location of release	Date of recovery	Location of recovery	Days out	Distance traveled (miles)	Average daily rate (miles)
'58-7-1	50-59 N, 168-22 E	'58-8-7	51-21 N, 159-34 E	37	330	8.9
'58-7-1	50-59 N, 168-22 E	'58-7-24	51-43 N, 159-33 E	23	334	14.5
'58-7-6	51-52 N, 164-38 E	'58-7-31	49-06 N, 157-24 E	25	314	12.6
'58-7-6	51-52 N, 164-38 E	'58-8-2	Ozernaia R., west Kam.	27	342	12.7
'58-7-6	51-45 N, 164-23 E	'58-8-5	Ozernaia R., west Kam.	29	340	11.7
'58-7-7	51-45 N, 164-23 E	'58-7-29	50-58 N, 154-05 E	22	384	17.5
'58-7-9	50-41 N, 164-34 E	'58-8-2	51-18 N, 154-15 E	24	380	15.8
'58-7-9	50-41 N, 164-34 E	'58-7-31	Ozernaia R., west Kam.	22	330	15.0
'59-5-26	48-00 N, 170-00 E	'59-7-1	52-44 N, 165-01 E	36	383	10.6
'59-5-29	45-53 N, 166-49 E	'59-6-25	50-40 N, 162-17 E	27	320	11.9
'59-5-31	43-54 N, 167-06 E	'59-6-28	49-24 N, 165-36 E	28	332	11.9
'59-6-5	48-00 N, 164-00 E	'59-7-15	Storozh R., east Kam.	40	490	12.3
'60-6-18	48-28 N, 170-45 E	'60-7-8	49-29 N, 164-24 E	20	305	15.3
'61-5-16	43-54 N, 160-58 E	'61-8-6	52-30 N, 166-30 E	92	560	6.1
'61-5-29	46-44 N, 164-23 E	'61-7-22	44-39 N, 154-01 E	54	455	8.4
'61-6-6	50-47 N, 166-51 E	'61-8-2	Krutogorova R., west Kam.	57	870	15.3
'61-6-10	48-55 N, 167-09 E	'61-7-29	Ozernaia R., west Kam.	49	463	9.4
Average rate				612	6932	11.33

[1] Rates are given in nautical miles per day, based on the shortest distance between points of tagging and recovery. These recoveries were selected for this table for reasons explained in the text.

that they were not of western Alaskan origin) and had travelled towards the Kamchatkan coast at least 300 nautical miles as measured by the shortest distance between tagging and recovery locations (distances less than 300 miles were excluded in order to avoid possible errors resulting from inaccuracies in ship reports of tagging and recovery locations).

The rates for the 17 fish were relatively uniform; they averaged 11.3 nautical miles per day and ranged from 6.1 to 17.5 miles per day.

So few recoveries as only 17 are not sufficient to permit detailed comparisons to be made between Kamchatkan and western Alaskan sockeye regarding rates of travel. However, the differences are so great that it would seem safe to conclude that during the last stages of their migration Bristol Bay sockeye travel at a much faster rate, or by a more direct route (or possibly a combination of both these factors), than do Kamchatkan sockeye.

Another recovery of a fish that was almost undoubtedly maturing and of Kamchatkan origin, and that had travelled a great distance before recapture, should be mentioned at this time. This fish was tagged on May 9, 1961, at 48°29′N, 159°10′W, and was recovered on July 2, 1961, at 50°47′N, 162°29′E. Its shortest migration route was therefore approximately 1,485 miles in 53 days, an average rate of 28 miles per day. That this fish was of Kamchatkan origin and maturing is probable on the basis of the fact that it was recaptured so far to the west at such a late date and because of its size and age (fork length 55.0 cm when tagged; age 6_3).

Maturing Sockeye in the Gulf of Alaska

There seems to be little doubt that calculations of the rate of travel of maturing sockeye salmon in the Gulf of Alaska are considerably less meaningful *per se* than in the cases cited above of maturing Bristol Bay sockeye tagged in the Aleutian area, or of Kamchatkan sockeye tagged to the southeast of the Kamchatka Peninsula. There are probably two main reasons for this. In the first place, it is known from Canadian researches in the Gulf in 1961 and 1962 that the sockeye remain concentrated in the west-central region of the Gulf for a considerable period of time during the spring and early summer before they begin to move out of the Gulf towards their areas of origin. Plankton studies (LeBrasseur, 1965) have indicated that this is probably an important feeding area. Secondly, and based mainly on the results of Canadian taggings in the Gulf in 1962, it is believed that there can be some considerable movement in the Gulf, mainly in a northerly direction, prior to any more direct movement towards the final destination. In the case of pink salmon from central British Columbia, for example, the 1962 Canadian taggings clearly demonstrated that many pinks first migrated far to the north beyond central British Columbia, and then turned south to return to that area. There were indications, too, that Fraser River sockeye moved northward over a broad front in the Gulf, and that probably this was followed by an eastward movement into coastal waters, and then again by a southward migration to the Fraser River, either by way of Johnstone Strait-Strait of Georgia, or via the Strait of Juan de Fuca.

These points must therefore be kept in mind when examining the computations that are presented in this section, which are, of course, based upon measurements of the shortest distance between points of tagging and recovery. Examples of the apparent rate of migration of maturing sockeye in the Gulf of Alaska have been extracted from the Canadian tagging data for 1962, using all recoveries to the following selected areas: Kodiak Island; Copper River; the Nass-Skeena fishing area; the Fraser River (including recoveries in Johnstone Strait-Strait of Georgia and in Juan de Fuca Strait). These are summarized in Table 5.

TABLE 5. Rates of migration of maturing sockeye salmon tagged in the Gulf of Alaska by Canada, 1962[1].

Tagging period	Recovery area			
	Kodiak Island	Copper River	Nass-Skeena rivers	Fraser River
April 9–May 24				
No. of fish recovered	25	43	33	39
Average rate—miles	7.1	9.2	8.6	10.2
Range	4.0 –14.3	3.0 –25.0	3.9 –21.6	6.0 –20.7
May 28–June 30				
No. of fish recovered	35	4	11	38
Average rate—miles	7.7	17.2	15.8	15.2
Range	3.0 –27.1	10.3 –32.7	10.4 –28.2	6.4 –30.0
July 3–27				
No. of fish recovered	8	0	11	27
Average rate—miles	12.5	—	19.8	16.1
Range	4.9 –19.3	—	10.0 –40.0	8.2 –33.8

[1] Rates are given as nautical miles per day, based on the shortest distance between points of tagging and recovery.

From Table 5 it can be seen that all the calculated rates are very low in comparison with the recoveries in Bristol Bay of fish tagged in the Aleutian area or in the Bering Sea. In the later periods they are more comparable with the presumed Bristol Bay sockeye that were recovered in the Japanese mothership fishery, and with the 17 Kamchatkan sockeye, as described earlier.

It will also be noted that the apparent rate of travel increased the later the fish were tagged. With one exception, this occurred not only with the average rate but also with both the lower and upper limits of each range.

In addition to the data presented in Table 5, it is of interest to record the calculated rates of travel of three maturing sockeye of British Columbia origin that were tagged to the west of the Gulf of Alaska:

(a) Tagged June 25, 1959, at 49°47′N, 176°42′W; recovered at Somerville Island, Nass River, on August 19, 1959. Distance travelled, 1,720 miles; days out, 55; average rate of travel, 31.3 miles per day.

(b) Tagged May 22, 1961, at 49°04′N, 164°36′W; recovered at Rivers Inlet on July 26, 1961. Distance travelled, 1,390 miles; days out, 65; average rate of travel, 21.4 miles per day.

(c) Tagged May 14, 1962, at 49°07′N, 163°18′W; recovered at San Juan Islands on August 14, 1962. Distance travelled, 1,600 miles; days out, 92; average rate of travel, 17.4 miles per day.

The Canadian tagging of 1962 has also provided data for computations of rates of travel of 68 Bristol Bay sockeye that were tagged in the Gulf of Alaska. The calculations were based on the assumption that each fish had entered the Bering Sea by way of Unimak Pass. These data are summarized below:

	No. of fish	*Average rate*	*Range*
Early tagging, Apr. 9–May 6	37	12.7	7.9–20.0
Middle tagging, May 10–24	15	18.2	12.3–27.0
Late tagging, May 28–June 13	16	22.8	16.8–33.5

It will be noticed again both with the three British Columbia fish and the 68 Bristol Bay fish that those tagged earliest showed the slowest rate of travel, while those tagged latest showed the fastest rate of travel. In the case of the Bristol Bay fish this characteristic applies to both the upper and the lower limits of the range for each period.

GEOGRAPHICAL ORIGIN OF SOCKEYE ON THE HIGH SEAS

Evidence from Tagging

Purpose and Limitations of Tagging Experiments

The determination by the tagging method of the oceanic distribution of specific stocks of sockeye salmon depends upon the very strong tendency among them to return from the sea to their natal streams. In actual fact, tagging of individual fish only provides information related to the point of tagging and the point of recovery. It is the consistency of a pattern of recovery that permits reasonable conclusions to be drawn regarding either their geographical origin if recovered in coastal waters or in streams, or of migration routes if recovered on the high seas. However, "straying" may occur among returning salmon, so that in the case of isolated recoveries that possibility cannot be ignored. Also, fish may be recovered within coastal waters at points that are still distant from their original streams; again, only the consistency of a pattern of recovery provides for reasonable conclusions to be made regarding these.

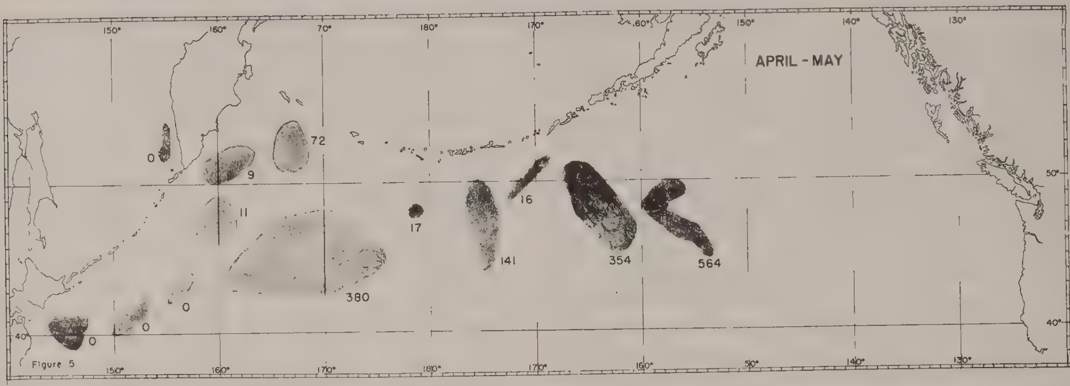
The use of tagging recoveries to make quantitative determinations of the extent of intermingling or the degree of dominance regarding specific stocks that are present together in ocean areas is a more difficult problem. This is mainly because differences occur between stocks in the intensity of fishing effort, in tag recovery effort and in the reporting of recovered tags. Also, the mortality rate from tagging can differ between groups of tagged fish due to differences between them in size, condition and in the time required to reach their final destination. Finally, it is only when coastal fishing is conducted close to the spawning streams in question that recoveries in coastal waters can reasonably be taken to indicate the point of origin.

Because salmon range widely and make extensive migrations during their last weeks in the sea, tagging must be conducted over broad areas and for prolonged periods in order to determine completely the oceanic distribution of given stocks. Furthermore, the rate of recovery of fish tagged on the high seas is very low, so that large numbers must be tagged in order to provide enough of the required information and, in particular, the consistency of recovery pattern that has been referred to.

In recent years the United States, Japan and Canada have carried out extensive tagging experiments that have ranged across the width of the North Pacific Ocean and throughout much of the Bering Sea. The results of these experiments will now be summarized and explained, so that the oceanic distribution of the important stocks of sockeye salmon that occur in Asia and North America may then be described.

Methods

The Japanese carried out some tagging experiments prior to 1958 in the western North Pacific using gillnets of synthetic fiber to catch the salmon (Kondo *et al.*, 1965)[2]. These were not very successful. Although substantial numbers of fish were tagged,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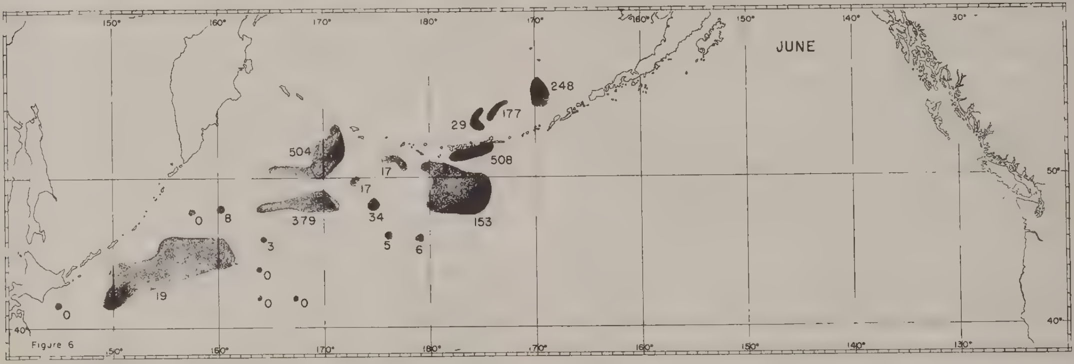
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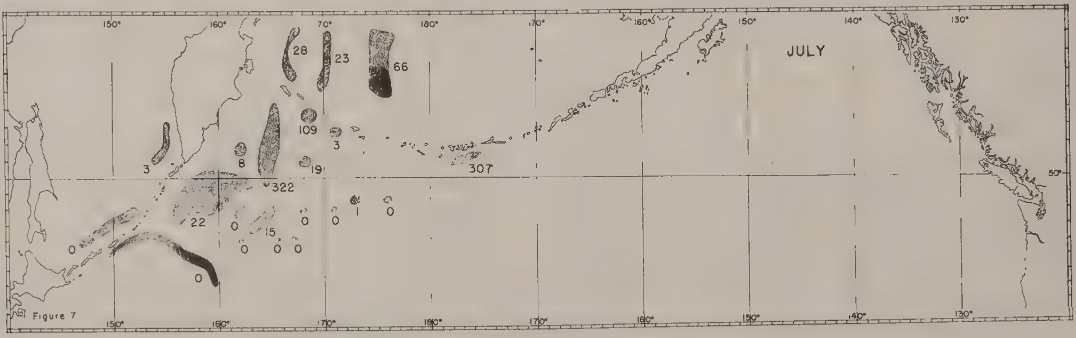
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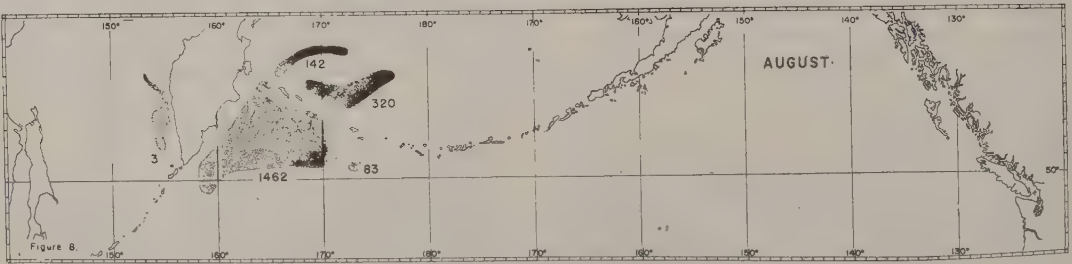
50°


AUGUST
142
320
3
1462
83
Figure 8.
150°
160°
170°
180°
170°
160°
150°
140°
130°
50°

FIGURES 5–8. Numbers of maturing and immature sockeye salmon tagged by Japan, 1958–62, by month.

mortality rates were very high because of injuries incurred by the fish when they were gilled; the recoveries were extremely few.

The Japanese first used longlines for high seas tagging in 1958 and they have employed them each year since then with considerable success. This gear consists of a main cotton line supported at the surface by floats, from which are suspended short nylon gangions with a hook attached. The preferred bait has been dry, salted anchovy. Up to 2,000 or more hooks have been used at one time. Although tagging by Japan has been conducted mainly in western North Pacific waters, it has on occasion extended far offshore to as far east as approximately 153°W.

Canada has also used the Japanese longline for high seas tagging, having purchased both gear and anchovy bait in Japan. Canada has tagged salmon in the Gulf of Alaska since 1961, fishing to as far west as 160°W and mainly northwards of 45°N.

The United States carried out exploratory tagging operations in the northern Gulf of Alaska in 1955, using purse seines to catch salmon in offshore waters. United States tagging has been extensive each year since then, particularly in the vicinity of the Aleutian Islands westward to Attu Island and in 1962 also in the Gulf of Alaska. The United States has consistently and successfully used large purse seines to catch salmon for tagging; this gear has been described in detail by Hartt (1962).

From 1956 to 1959 the tags used by the United States and Japan were mainly vinyl tubes and Petersen-type discs. However, in 1960 both countries began to use the disc tag almost exclusively, with the exception that the United States now uses small-diameter dart tags for very small, immature fish. Canada has used the Petersen-type disc tag exclusively in high seas tagging.

The tagging operation followed by each of the three countries has been to measure the fork length of the fish, take a scale sample for age and possible racial determination, record the species, tag number and condition of the fish, and release it as quickly as possible. At times, and especially involving fish in poor condition, samples have been retained for the determination of the condition of maturity and for food studies.

Numbers of Sockeye Tagged by Japan

Figures 5–8 show, by month of tagging, the numbers of maturing and immature sockeye tagged by Japan during the years 1958–62 combined. Over this period Japan tagged a total of 6,607 sockeye: 1,564 in late April–May, 2,107 in June, 926 in July and 2,010 in August.

In late April–May sockeye were tagged in the North Pacific from off southeast Kamchatka and Hokkaido to as far east as about 153°W, most of them between 43°N and 50°N. Fishing in the Okhotsk Sea off the west coast of Kamchatka, and to the east of Hokkaido to about 158°E, provided no fish for tagging.

In June, fishing directly east of Hokkaido and the southern Kuril Islands gave extremely few fish for tagging. With the exception of some tagging in the eastern Bering Sea, tagging during June was concentrated farther to the west than in May and mainly much closer to the Aleutian Islands. About 450 sockeye were tagged in the eastern Bering Sea, fairly close to the Aleutians, between 176°W and 168°W, approximately.

During July, about half of the sockeye tagged in the North Pacific were caught in two principal areas —directly south of Adak and off southeast Kamchatka. Only a few sockeye were tagged farther south and eastward of the Kurils, and only three in the Okhotsk Sea off the west coast of Kamchatka. Some sockeye were tagged in three regions of the western Bering Sea, roughly from 165°E to 175°E and northward to about 58°N.

With the exception of three fish tagged in the Okhotsk Sea, again off west Kamchatka, tagging in August was restricted to waters off southeastern Kamchatka westward of 173°E and in the western Bering Sea in an area similar to that covered in July.

Thus the tagging of sockeye salmon by Japan during 1958–62 may be described as having been most extensive during May in the North Pacific, extending to well offshore from the Aleutians to as far east as waters of the western Gulf of Alaska. Tagging in later months was mainly progressively farther to the west and closer to the Aleutian Islands. Some sockeye were tagged in the Bering Sea during June or later in two general areas, west of about 175°E and east of about 175°W. A very few sockeye were tagged (in 1962) in the Okhotsk Sea off west Kamchatka and, despite considerable effort, only a few in waters west of 160°E off Hokkaido and the Kuril Islands.

Numbers of Sockeye Tagged by the United States in the North Pacific and Bering Sea

Maturing fish. The numbers of maturing sockeye tagged by the United States in waters west of 160°W are shown by month of tagging for the period 1956–62 combined in Figures 9–12. Separation of maturing from immature sockeye was determined by the

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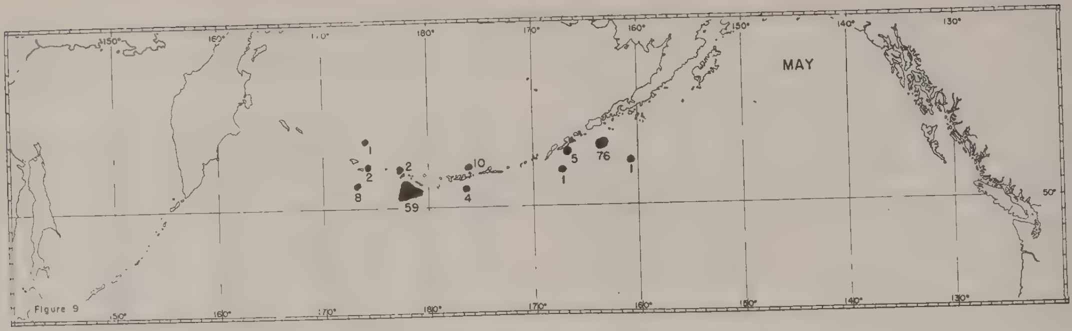
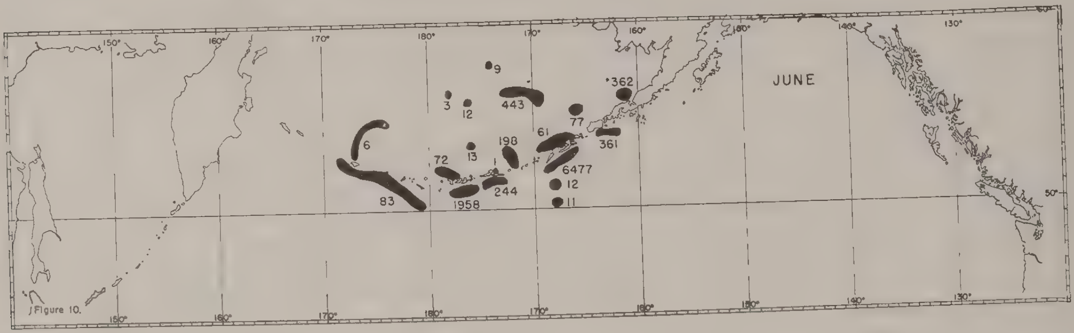
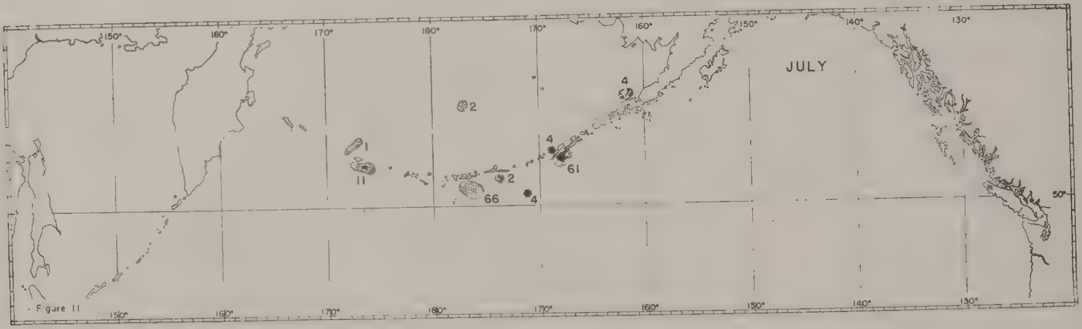
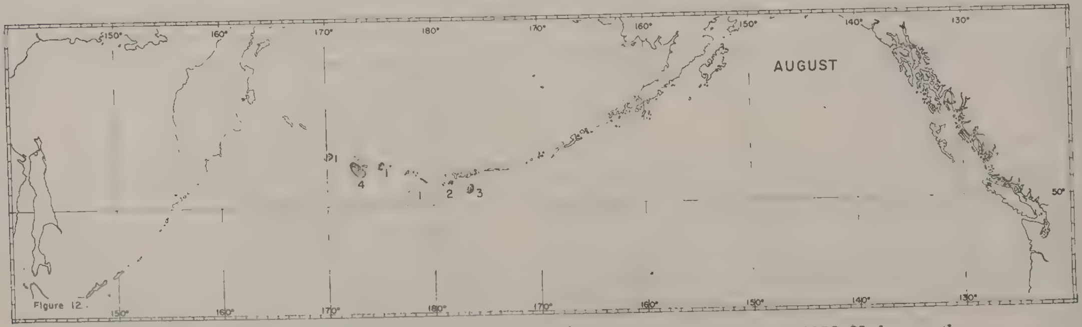
[2] This report was not available when our paper was written. Its subsequent publication enabled us to cite it in several instances, but we have not had an opportunity to consider it in detail.


MAY
150°
160°
170°
180°
170°
160°
150°
140°
130°
50°
1
2
2
8
59
10
4
5
1
76
1
Figure 9


JUNE
150°
160°
170°
180°
170°
160°
150°
140°
130°
50°
9
362
3
12
443
77
6
61
361
198
13
72
6477
12
244
83
1958
11
Figure 10.


JULY
150°
160°
170°
180°
170°
160°
150°
140°
130°
50°
4
2
1
4
11
61
2
66
4
Figure 11


AUGUST
150°
160°
170°
180°
170°
160°
150°
140°
130°
50°
1
4
1
1
2
3
Figure 12

FIGURES 9–12. Numbers of maturing sockeye salmon tagged by the United States, 1956–62, by month.

method described by Hartt (1962), which was based primarily on comparisons of the lengths of fish at time of tagging with the lengths at tagging of definitely maturing fish that were recaptured later in the same year in coastal fisheries and streams.

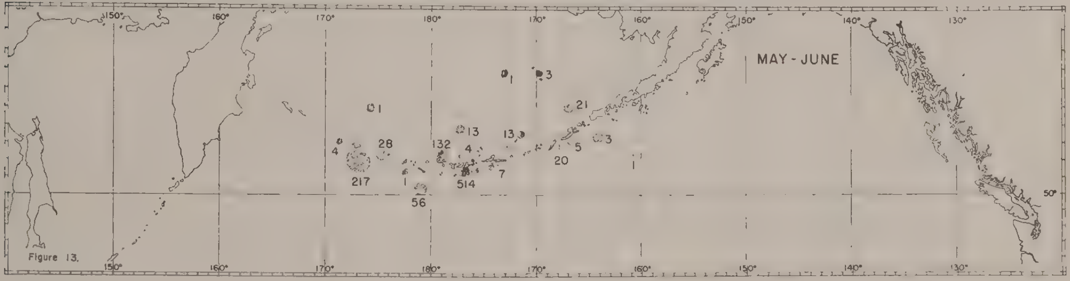
Over the period 1956–62, in the Bering Sea and in North Pacific waters west of the Gulf of Alaska (west of 160°W), the United States tagged a total of 10,740 maturing sockeye salmon: 169 in May, 10,403 in June, 156 in July and 12 in August.

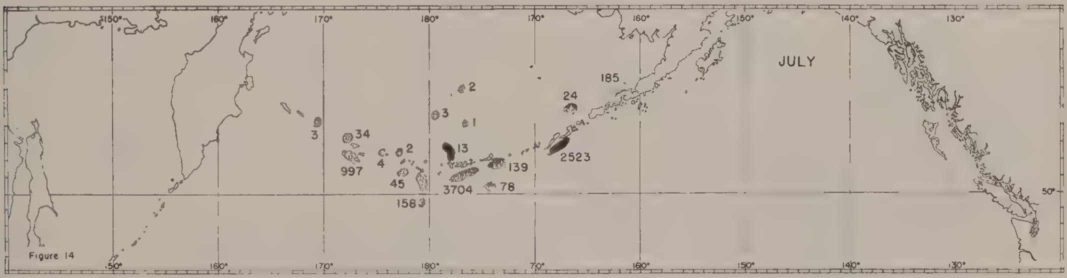
The 169 fish tagged in May were taken at widely scattered locations, but mainly at two positions, shown in Figure 9.

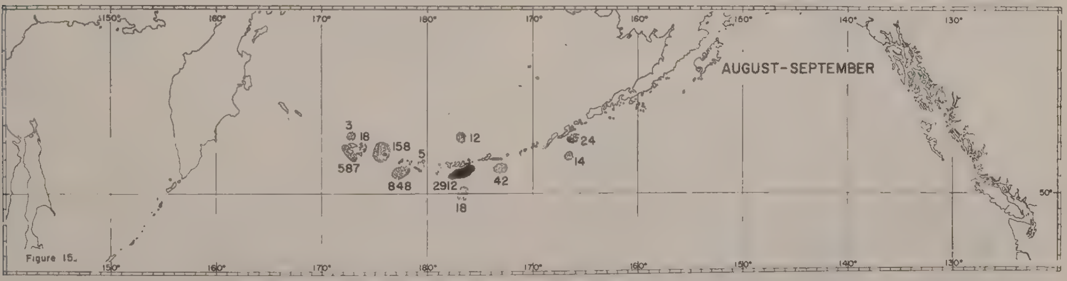
More than 95% of the total number of maturing sockeye tagged during 1956–62 were tagged in June. There were two principal areas of tagging which accounted for about 80% of the fish tagged in June—directly south of and mostly close to Unimak and Unalaska islands and directly south of and close to Adak Island (Fig. 10). Outside of the Bering Sea, with a few exceptions, almost all of the remaining fish tagged were also taken close to the Aleutian Chain, at points extending from 162°W to 172°E, approximately. Tagging locations in the Bering Sea were more scattered, but about two-thirds of the fish were released at points close to the northern shores of the Aleutian Chain and the Alaska Peninsula. Almost 500 fish were tagged in the vicinity of the Pribilof Islands.

The 156 fish tagged in July were released from widely scattered points, most of them from south of the Aleutians (Fig. 11).

The 12 fish tagged in August were caught at locations extending from about 170°E to 176°W, south of


MAY - JUNE
150°
160°
170°
180°
170°
160°
150°
140°
130°
50°
1
3
1
21
13
13
132
4
28
4
3
5
20
7
1
217
514
56
Figure 13.


JULY
150°
160°
170°
180°
170°
160°
150°
140°
130°
50°
2
185
24
3
1
3
34
2
13
997
4
139
2523
45
3704
78
1583
Figure 14


AUGUST-SEPTEMBER
150°
160°
170°
180°
170°
160°
150°
140°
130°
50°
3
18
158
12
24
5
14
587
848
2912
42
18
Figure 15.

FIGURES 13–15. Numbers of immature sockeye salmon tagged by the United States, 1956–62, by month.

the Aleutian Chain.

In summary then, during 1956–62 approximately 95% of the maturing sockeye tagged by the United States in the Bering Sea and North Pacific Ocean exclusive of the Gulf of Alaska were tagged in the month of June. The great bulk of these were tagged within about 50 miles of the southern shores of Adak, Unimak and Unalaska islands. The remaining releases in the North Pacific were relatively close to the Aleutians and extended from near Attu Island in the west to the tip of the Alaska Peninsula in the east. Taggings in the Bering Sea were widely scattered, with most fish having been released at two locations—near the Pribilof Islands and just north of the Alaska Peninsula.

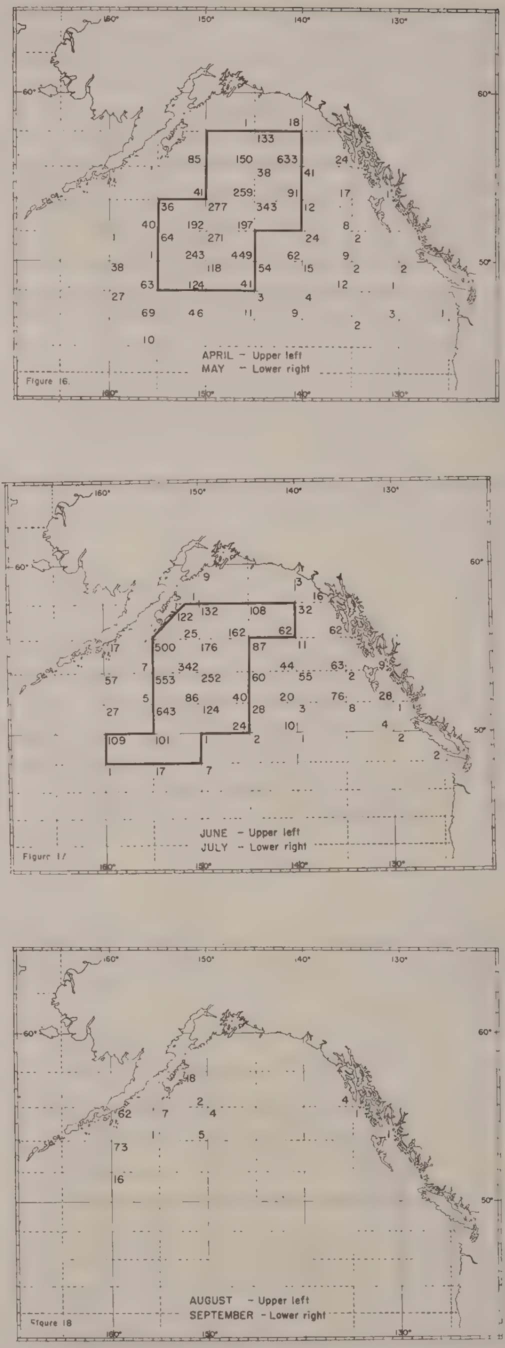
Immature fish. Figures 13–15 show the numbers and release locations of immature sockeye salmon tagged by the United States in the Bering Sea and in the North Pacific Ocean exclusive of the Gulf of Alaska during 1956–62. Altogether, 13,600 immature sockeye were tagged: 19 in late May, 1,025 in June, 7,915 in July, 4,482 in August and 159 in early September.

During June (including 19 tagged in late May), tagging of immature fish was conducted mainly relatively close to the Aleutian Islands in the North Pacific, at locations extending from Attu Island in the west to Atka and Amlia Islands in the east. Less than 200 were tagged in the Bering Sea, and at widely scattered locations, but mainly relatively close to the Aleutian Islands.

The distribution of the taggings of immature sockeye in July was very similar to that in June. Again, most of the immatures were tagged in the North Pacific from Attu to Amlia, close to the Aleutian Chain, and again only relatively few were tagged in the Bering Sea, at scattered locations. Among the latter, those tagged immediately north of the Alaska Peninsula were almost all fish which had just entered the sea.

The August–early September distribution of taggings of immatures remained similar to those in earlier months, with the exception that fewer were tagged east of Adak in the North Pacific, and extremely few were tagged in the Bering Sea.

Thus about 90% of all the immature sockeye tagged during 1956–62 by the United States were released during the months of July and August; most of these were tagged close to the southern shores of the Aleutian Islands from Attu Island in the west to Amlia Island in the east. A few were tagged farther offshore in the North Pacific, and small numbers were tagged at widely scattered points in the Bering Sea, again mainly relatively close to the



FIGURES 16–18. Numbers of sockeye salmon tagged by the United States and Canada in the Gulf of Alaska, 1956–62, by month.

Aleutian Chain.

Numbers of Sockeye Tagged by Canada and the United States in the Gulf of Alaska

Major tagging of salmon in offshore waters of the Gulf of Alaska (that is, east of 160°W) was started by Canada in 1961, using Japanese longline gear; in 1962 both Canada, again using longlines, and the United States, using purse seines, tagged there. Canada tagged approximately 6,900 sockeye and the United States tagged 2,300 in these two years. In addition, small numbers of sockeye were tagged in the Gulf in earlier years by United States vessels as they were en route to or from the Aleutian area of tagging operations.

Figures 16–18 show the numbers of sockeye tagged in each month of the combined 1956–62 period grouped in 2° Latitude by 5° Longitude rectangles. This grouping into rectangles has been done in order to simplify the presentation of taggings at numerous locations all over the Gulf, north of 44°N.

As yet, except in a few instances, a satisfactory method of distinguishing between maturing and immature fish tagged in the Gulf has not been developed. Thus the figures shown apply to a mixture of both kinds of fish.

The greatest numbers of sockeye were tagged in the month of June (3,251), but large numbers were also tagged in April (1,507), May (2,911) and July (1,058). Only 181 were tagged in August and nine in September.

In April and May the heaviest tagging of sockeye took place in the central region of the Gulf within the area indicated by the heavy line shown in Figure 16. Roughly speaking, this area lay between 140°W and 155°W and from 48°N to 58°N. Considerably smaller numbers of sockeye were tagged in all directions outside of this central region.

In June and July the region of most intensive tagging lay within the boundaries indicated by the heavy line in Figure 17. This region lies farther to the west than that shown for April and May.

During August and September small numbers were tagged near the southeastern Alaska-northern British Columbia coast and in the northwestern region of the Gulf, as is shown in Figure 18.

The Distribution of Stocks of Maturing Sockeye

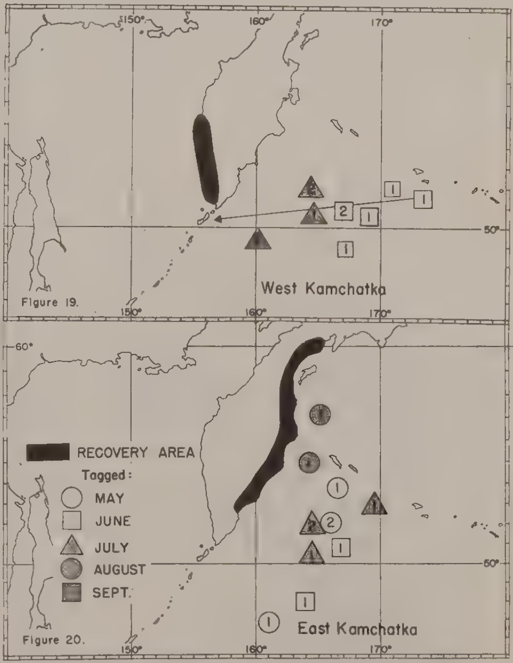
The known oceanic distribution of maturing sockeye salmon from Asian and North American territories is based upon the recoveries in coastal fisheries or in fresh water of fish tagged at sea. It is assumed that these fish had returned to their natal streams or were returning there when intercepted.

The illustrations and data presented in this section are primarily the results of taggings conducted by the United States, Japan and Canada during 1956–62. However, some recoveries from taggings by Japan in earlier years have also been included (Hirano, 1953) so that these data form a complete record of all coastal recoveries of maturing sockeye tagged in offshore waters of the North Pacific Ocean and Bering Sea up to 1962.

West Kamchatkan sockeye. Figure 19 shows the distribution at tagging of maturing sockeye recovered in west Kamchatka. There have been nine recoveries to this area, plus one in a coastal fishery near the Kuril Strait in 1938. The numbers recovered by year and month of tagging are as follows:

	June	*July*
1938	1	—
1958	—	3
1959	—	1
1960	1	—
1961	4	—
Total (10)	6	4

The distribution of these fish when tagged lay between 49°N and 52°N, and extended from approximately 160°E to 173°30′E. Although they were not



FIGURES 19–20. Tagging locations of maturing sockeye salmon recovered in west and east Kamchatka, up to 1962.

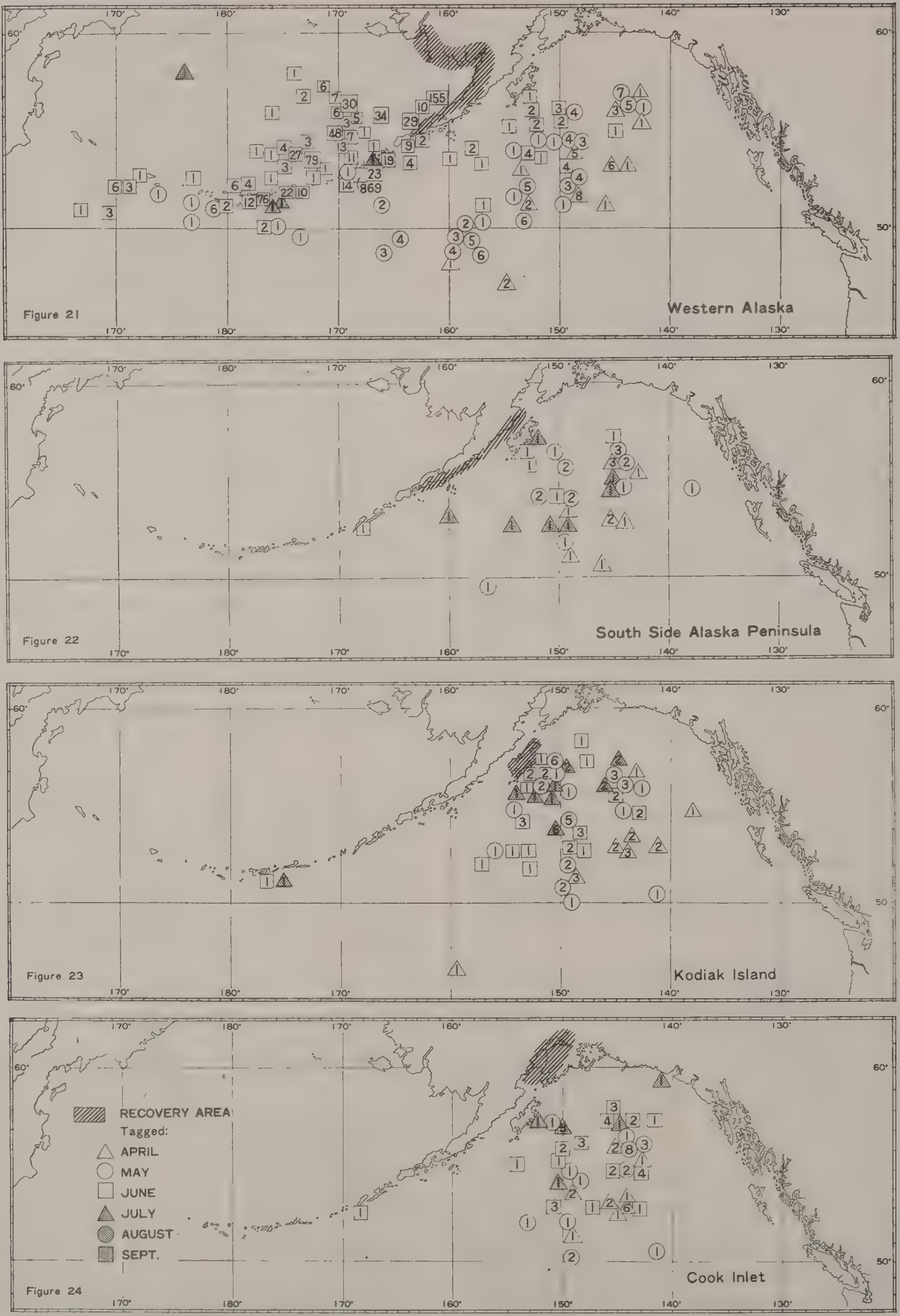


Figure 21
Western Alaska
Figure 22
South Side Alaska Peninsula
Figure 23
Kodiak Island
Figure 24
Cook Inlet
▨ RECOVERY AREA
Tagged:
△ APRIL
○ MAY
☐ JUNE
▲ JULY
● AUGUST
▩ SEPT.
170°
180°
170°
160°
150°
140°
130°
60°
50°

FIGURES 21–24. Tagging locations of maturing sockeye salmon recovered in western Alaska, the south side of the Alaska Peninsula, Kodiak Island, and Cook Inlet, up to 1962.

tagged in the same years, it is evident that the "July" recoveries were tagged closer to the Kamchatkan coast than were the "June" recoveries.

East Kamchatkan sockeye. The distribution at tagging of recoveries in east Kamchatka is shown in Figure 20. There have been 12 recoveries; the numbers by year and month of tagging are as follows:

	May	*June*	*July*	*August*
1941	1	—	—	—
1955	—	—	—	1
1956	—	—	1	—
1958	—	—	3	1
1959	—	1	—	—
1961	—	1	—	—
1962	3	—	—	—
Total (12)	4	2	4	2

The ocean distribution of these fish is relatively limited, as was the case with the west Kamchatkan fish. It lies between 47°N and 57°N, approximately, and from 170°E to about 161°E.

Western Alaskan sockeye. Recoveries from western Alaska include all recoveries from the north side of the Alaska Peninsula and farther north, including Bristol Bay and the Kuskokwim River. The distribution at tagging is shown in Figure 21. There have been 1,731 such recoveries up to 1962.

The numbers recovered by year and month of tagging are as follows:

	April	*May*	*June*	*July*
1956	—	—	82	1
1957	—	—	47	—
1958	—	1	40	1
1959	—	1	25	1
1960	—	9	580	1
1961	2	30	766	—
1962	30	48	66	—
Total (1,731)	32	89	1,606	4

Figure 21 makes it immediately apparent that an extremely wide east-west oceanic distribution has been demonstrated for maturing western Alaskan sockeye. This has extended from approximately 167°E in the western North Pacific to about 142°30′W in the Gulf of Alaska.

Their north-south distribution may be described according to three divisions—in the North Pacific west of 160°W, in the Gulf of Alaska from 160°W eastwards, and in the Bering Sea.

In the North Pacific to the west of the Gulf of Alaska almost all recoveries, with a few marked exceptions, were from fish tagged very close to the Aleutian Islands and the tip of the Alaska Peninsula. This fact reflects the locations of most of the tagging conducted by the United States during 1956–62. The southernmost tagging in this general area which produced recoveries was at approximately 48°N, 166°W (three fish tagged by Japan in 1961).

The scarcity of recoveries from releases south of 50°N, between 160°W and 170°E, is at least partly due to the paucity of tagging in that area. Some tagging was done by Japan in this region during April and May of 1961, but only the few recoveries shown resulted.

In the Gulf of Alaska the north-south distribution at tagging of fish recovered in western Alaska extended from approximately 46°N (at 155°W) to 57°N (at 145°W). It should also be noted that in the Gulf the most northerly releases of fish recovered in western Alaska were also those farthest to the east, while, with one exception, the most southerly releases were also those farthest to the west. Most of the fish tagged in the Gulf of Alaska and recovered in western Alaska were tagged by Canadian operations in 1962. In that year, therefore, the results indicate that western Alaskan sockeye were distributed in the Gulf over a broad northeast-southwest front. As was described in a preceding section, the movement of these fish out of the Gulf occurred over this broad front in a northwesterly direction, and was completed early in the season since there were no recoveries from taggings later than about mid-June.

With one exception (tagged in July) all the western Alaskan recoveries from the Bering Sea releases had been tagged in June. Release points of these June recoveries extended from close to the Aleutian Islands northwards to about 58°N (at 174°W). The July recovery had been tagged farthest to the west, at approximately 176°E (at 58°N).

Sockeye along the south side of the Alaska Peninsula. These recoveries are shown in Figure 22. Based on the results of taggings by the United States in earlier years (Gilbert, 1923; Gilbert and Rich, 1925) it is probable that some, perhaps many, of these recoveries were of fish en route to western Alaskan streams. However, these recoveries also include fish of Chignik origin, including the one tagged farthest to the west, at about 168°W. Recoveries to this area came from taggings as far east in the Gulf of Alaska as approximately 138°W (at about 55°N) and from as far south in the Gulf as approximately 49°30′N (at 156°30′W).

Altogether there have been 37 recoveries; the numbers recovered by year and month of tagging are as follows:

	April	*May*	*June*	*July*
1956	—	—	1	—
1961	—	2	3	1
1962	10	13	1	6
Total (37)	10	15	5	7

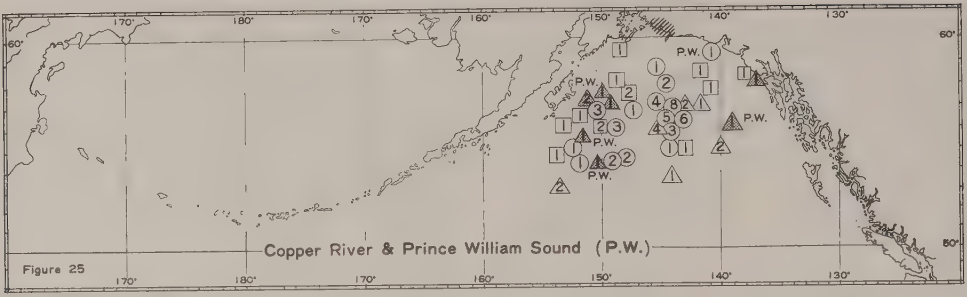


Figure 25
Copper River & Prince William Sound (P.W.)
P.W.
170°
180°
170°
160°
150°
140°
130°
60°
50°

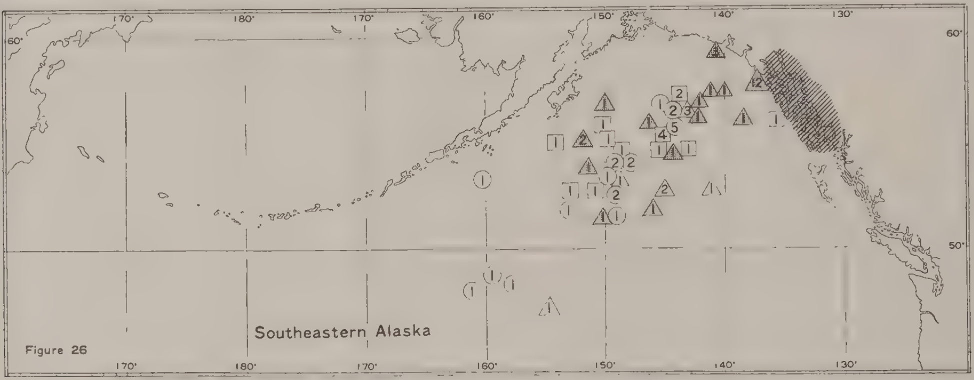


Figure 26
Southeastern Alaska
170°
180°
170°
160°
150°
140°
130°
60°
50°

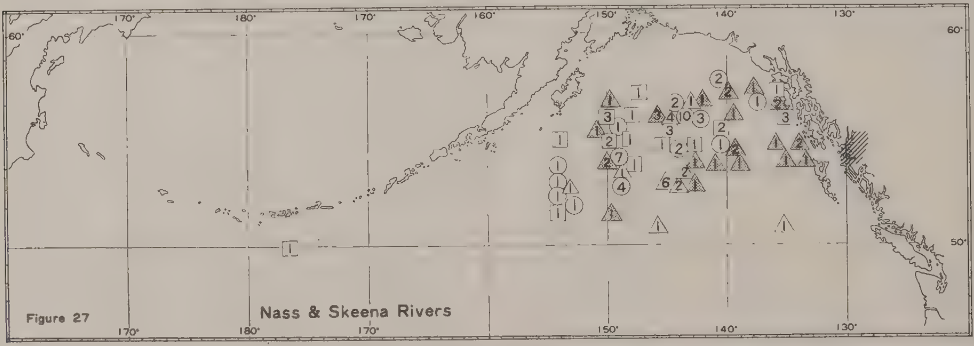


Figure 27
Nass & Skeena Rivers
170°
180°
170°
160°
150°
140°
130°
60°
50°

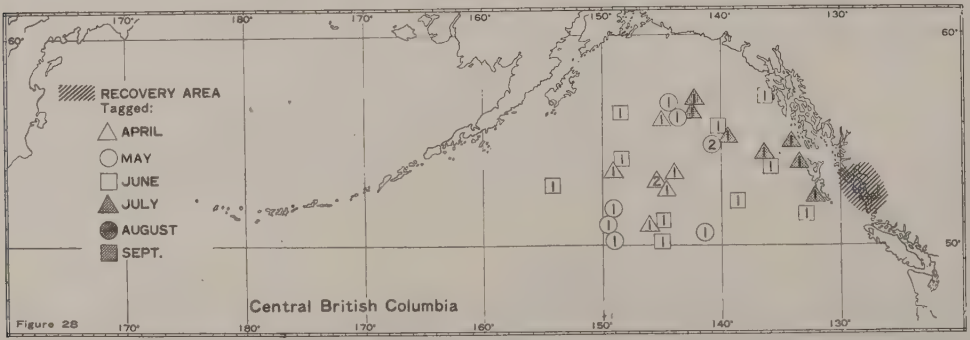


Figure 28
Central British Columbia
RECOVERY AREA
Tagged:
APRIL
MAY
JUNE
JULY
AUGUST
SEPT.
170°
180°
170°
160°
150°
140°
130°
60°
50°

FIGURES 25–28. Tagging locations of maturing sockeye salmon recovered in Copper River and Prince William Sound, southeastern Alaska, Nass and Skeena rivers, and central British Columbia, up to 1962.

Kodiak Island sockeye. Figure 23 illustrates the 89 recoveries from this area. The numbers recovered by year and month of tagging are as follows:

	April	*May*	*June*	*July*
1959	—	—	1	1
1961	—	1	4	4
1962	15	30	21	12
Total (89)	15	31	26	17

Recoveries from taggings farthest to the west were the two from tagging just south of Adak Island. The easternmost tagging resulting in a recovery in Kodiak was at 138°W (at 55°N), from which there was one isolated recovery. The southernmost tagging which provided a recovery in Kodiak, also an isolated one, was at about 46°N (at approximately 159°30′W). Thus, although during the tagging period the main concentrations of Kodiak Island sockeye were in the west-central region of the Gulf, these isolated recoveries have demonstrated a very widespread distribution of maturing Kodiak Island sockeye.

Cook Inlet sockeye. These recoveries have totalled 76; the numbers recovered by year and month of tagging are as follows:

	April	*May*	*June*	*July*
1961	—	—	9	7
1962	16	22	20	2
Total (76)	16	22	29	9

With one exception, all Cook Inlet recoveries came from taggings within the Gulf of Alaska (Fig. 24). The exception, that tagged farthest to the west, was taken close to the southern shore of Umnak Island (approximately 168°W). The most southerly and easterly taggings within the Gulf which yielded Cook Inlet recoveries were, respectively, at 50°N (at 149°W) and at 141°30′W (at 50°30′N).

Copper River sockeye. Copper River recoveries, illustrated in Figure 25, include several that were actually from Prince William Sound. There have been 77 recoveries to this area; the numbers recovered by year and month of tagging are as follows:

	April	*May*	*June*	*July*
1961	—	2	7	3
1962	12	42	6	5
Total (77)	12	44	13	8

All recoveries to the Copper River area came from fish tagged within the Gulf of Alaska. There were not only no recoveries from taggings farther west than 154°W, but also none from taggings farther south than 53°N. These fish showed a more northerly distribution early in the season than did other stocks from Gulf of Alaska territory. Also, as was described in a preceding section, they were amongst the earliest to move from offshore into coastal waters.

Southeastern Alaskan sockeye. The southeastern Alaskan recoveries (Fig. 26) include one to the region between the Copper River and Cape Spencer. There were 73 recoveries; the numbers recovered by year and month of tagging are as follows:

	April	*May*	*June*	*July*
1961	1	3	4	18
1962	7	18	11	11
Total (73)	8	21	15	29

The high seas distribution at tagging of these fish extended to approximately 161°W in the west (at about 47°30′N) and to approximately 46°30′N in the south (at about 154°30′W). However, all but five of the recoveries were of fish tagged in the more restricted zone bounded by approximately 51°N in the south and 154°W in the west.

The recoveries from the southernmost taggings (in the region of 160°W) were of fish tagged by Japan in April (1) and May (3) of 1961. Most of the remainder were tagged by Canada in 1962, and include fish tagged as early as in mid-to-late April to as late as the latter part of July.

Nass and Skeena rivers sockeye. These recoveries are shown in Figure 27. They number 105, including two that were actually from the Queen Charlotte Islands. The numbers recovered by year and month of tagging are as follows:

	April	*May*	*June*	*July*
1958	—	—	1	—
1959	—	—	1	—
1961	—	—	9	5
1962	19	37	12	21
Total (105)	19	37	23	26

A single recovery in the Nass-Skeena area resulted from releases as far west as approximately 177°W (at 50°N). The remaining recoveries all came from taggings well within the boundaries of the Gulf of Alaska, none being from tagging farther west than about 155°W nor farther south than approximately 51°N.

Most of these fish were tagged by Canada in 1962. A broad east-west distribution in the Gulf is evident. As was mentioned in an earlier section, these fish probably moved mainly northwards over this front during the spring and early summer, then eastward towards the coast. In many instances the fish must have then followed a southerly coastal migration in order to reach their final destinations.

Central British Columbia sockeye. This area (Fig. 28) lies between the Nass-Skeena rivers area and the

Rivers-Smith inlets area. Recoveries totalled 32; the numbers recovered by year and month of tagging are as follows:

	April	*May*	*June*	*July*
1961	—	—	1	—
1962	7	8	9	7
Total (32)	7	8	10	7

Recoveries in central British Columbia were all from fish tagged within the Gulf, from 154°W in the west (at 51°N) and from 50°N in the south (between 140°W and 150°W).

As with the Nass-Skeena fish, it is probable that a northward movement over a broad east-west front was followed by an eastward movement towards the coast and then, in some instances, by a southerly migration to the central British Columbia area.

Rivers and Smith inlets sockeye. Recoveries to this area are shown in Figure 29. They amounted to 73 and the numbers recovered by year and month of tagging were as follows:

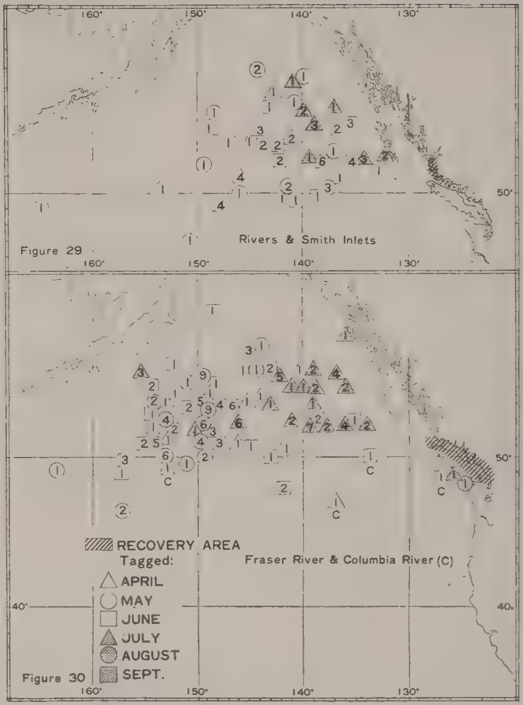
	April	*May*	*June*	*July*
1961	—	1	—	—
1962	18	15	26	13
Total (73)	18	16	26	13

All but one of the recoveries came from taggings within the Gulf of Alaska. The exception was tagged by Japan in May of 1961 at approximately 164°30′W and 49°N. The most southerly tagging which yielded a recovery in this area was at 47°N (at about 150°30′W). The movements of these fish in the Gulf before they reached their final destination were probably similar in the main to those described for the Nass-Skeena and central British Columbia sockeye.

Fraser River sockeye. The Fraser River recoveries total 163. These are illustrated in Figure 30, which also shows the tagging locations of four Columbia River recoveries. Also included are several recoveries, believed to have been fish en route to the Fraser River, that were made in coastal waters from 51°N southwards to Puget Sound. The numbers recovered by year and month of tagging are as follows:

	April	*May*	*June*	*July*	*August*
1958	—	—	2	3	—
1959	—	1	—	—	—
1961	—	—	3	2	1
1962	11	49	52	43	—
Total (167)	11	50	57	48	1

Fraser River recoveries have come from taggings conducted as far to the west as approximately 163°30′W (at about 49°N) and from as far to the south as 46°30′N (at 157°W).



FIGURES 29–30. Tagging locations of maturing sockeye salmon recovered in Rivers and Smith inlets, the Fraser River and approaches and the Columbia River, up to 1962.

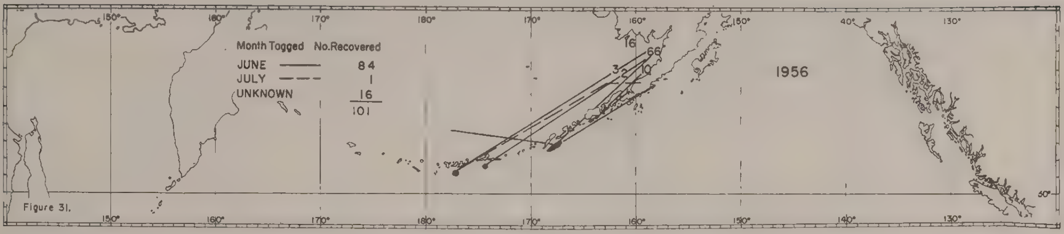
The distribution of Fraser River fish in the Gulf was over a broad east-west front and, on the average, was more southerly than that of stocks from farther north.

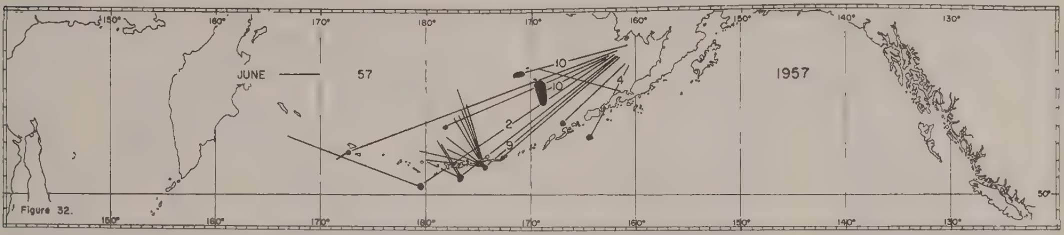
The tagging results here indicated that these fish, too, probably shift northwards in the Gulf early in the season, then make an eastward movement towards the coast during July, which would be followed by a southerly migration towards the Fraser River. Coastal taggings and observations of the progress of the commercial fisheries have indicated that some Fraser River sockeye return by way of the Strait of Juan de Fuca, while others return by way of Johnstone Strait and the Strait of Georgia.

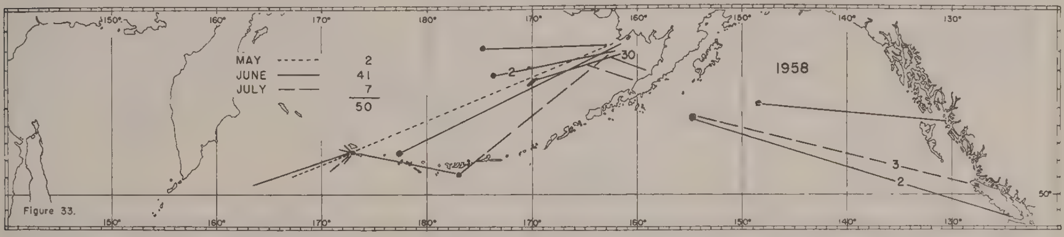
Figure 30 also shows that the four recovered Columbia River fish were widely dispersed from east to west when tagged, but that none was found north of 50°N.

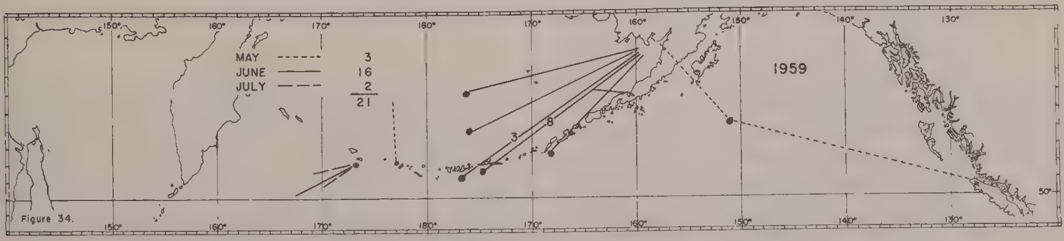
High Seas Recoveries of Maturing Sockeye

The high seas recoveries of sockeye salmon tagged by the United States and Japan during the years 1956–62


Month Tagged No.Recovered
JUNE 84
JULY 1
UNKNOWN 16
101
1956
16
66
3
10
Figure 31.
150°
160°
170°
180°
170°
160°
150°
140°
130°
50°


JUNE 57
1957
10
10
4
2
9
Figure 32.
150°
160°
170°
180°
170°
160°
150°
140°
130°
50°


MAY 2
JUNE 41
JULY 7
50
1958
30
2
3
2
Figure 33.
150°
160°
170°
180°
170°
160°
150°
140°
130°
50°


MAY 3
JUNE 16
JULY 2
21
1959
3
8
Figure 34.
150°
160°
170°
180°
170°
160°
150°
140°
130°
50°

FIGURES 31–34. High seas and coastal recoveries of maturing sockeye salmon, United States tagging, 1956–59.

are illustrated in Figures 31 to 42. These figures also show the coastal recoveries that were made, since these are important in making the general interpretations of the high seas recoveries which will be attempted briefly in this section.

There have been numerous high seas recoveries during 1956–62, but it must be realized that their interpretation relative to their continental origin is frequently either impossible or difficult. In actual fact, it is not at all possible from tagging data alone to be certain of the continental origin of any individual salmon that is recovered in offshore waters. However, some general conclusions can be made when a number of high seas recoveries fit into a pattern that is obviously compatible with the apparent route of migration to some final destination that has been demonstrated by a significant number of actual coastal recoveries.

It is not the intent in this section to discuss in detail the significance of the high seas recoveries that are illustrated in Figures 31 to 42, mainly because their interpretation would be dependent upon the inclusion

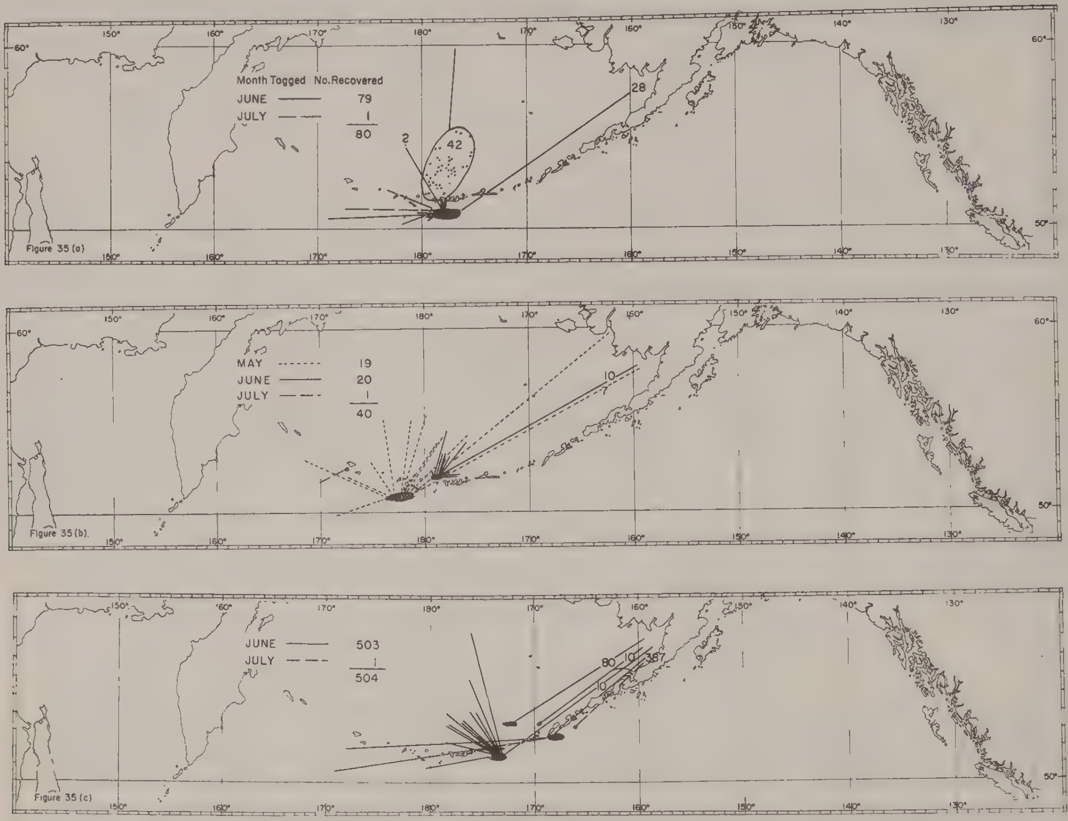


FIGURE 35. High seas and coastal recoveries of maturing sockeye salmon, United States tagging, 1960, by tagging areas.

of much more information than can be dealt with here—in particular, the seasonal distribution each year of the Japanese mothership fishery. Also, the data available at this time do not allow certainty in each case that the recovered sockeye was actually maturing. Indeed, there were a number, particularly from among some of those tagged far to the west, that were probably immature fish that happened to be recovered in the same year they were tagged.

With these points in mind some generalizations will be attempted regarding the significance of the high seas recoveries, treating the taggings by the United States and Japan separately. There were no high seas recoveries of sockeye salmon from Canadian taggings in the Gulf of Alaska in 1961 and 1962.

United States tagging, 1956–62. Detailed descriptions of the high seas recoveries of maturing sockeye salmon tagged by the United States during 1956-60 have been made by Hartt (1962, 1966).

In an earlier section of this report the direction of movement of maturing sockeye salmon in the Aleutian area was described on the basis of information obtained from tag recoveries and from the direction of the opening of the net in the United States seining operations. It was shown that there was a strong westward movement of maturing sockeye close to the southern shores of the Aleutian Islands, and that Bristol Bay sockeye entered the Bering Sea by way of the Aleutian passes and then migrated in a general easterly direction towards Bristol Bay, apparently on occasion over a broad north-south front.

The pattern of recoveries from taggings in the Aleutian area, both south of the Aleutians and in the Bering Sea, together with information on direction of movement obtained from seine sets, indicates clearly that at least the majority of the recoveries made in the Japanese mothership fishery operating north of the Aleutians was Bristol Bay fish. This conclusion is best confirmed by referring to the illustrations for 1957, 1960 and 1961 (Figs. 32, 35, 36) when considerable

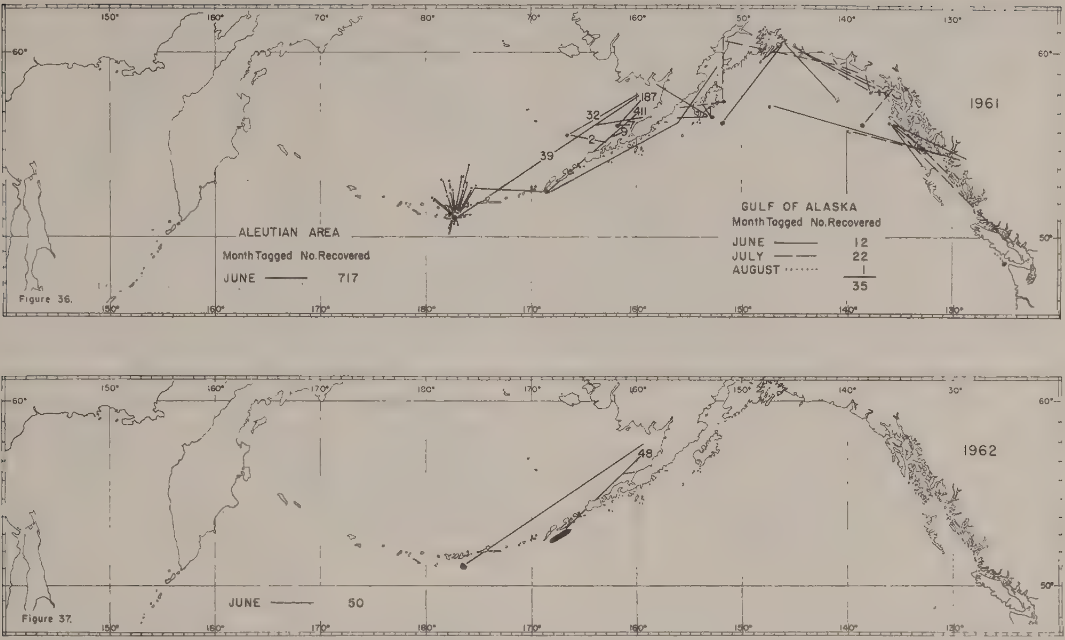


Figure 36.
1961
ALEUTIAN AREA
Month Tagged No. Recovered
JUNE 717
GULF OF ALASKA
Month Tagged No. Recovered
JUNE 12
JULY 22
AUGUST 1
35
187
411
32
5
2
39
Figure 37.
1962
48
JUNE 50
150°
160°
170°
180°
170°
160°
150°
140°
130°
60°
50°

Figures 36–37. High seas and coastal recoveries of maturing sockeye salmon, United States tagging, 1961 and 1962.

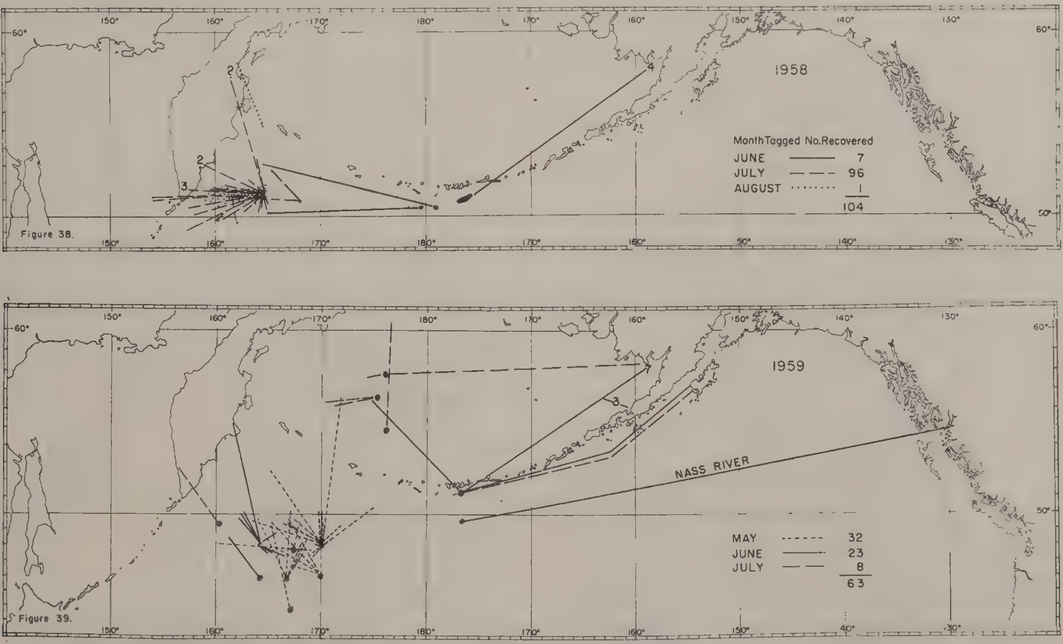
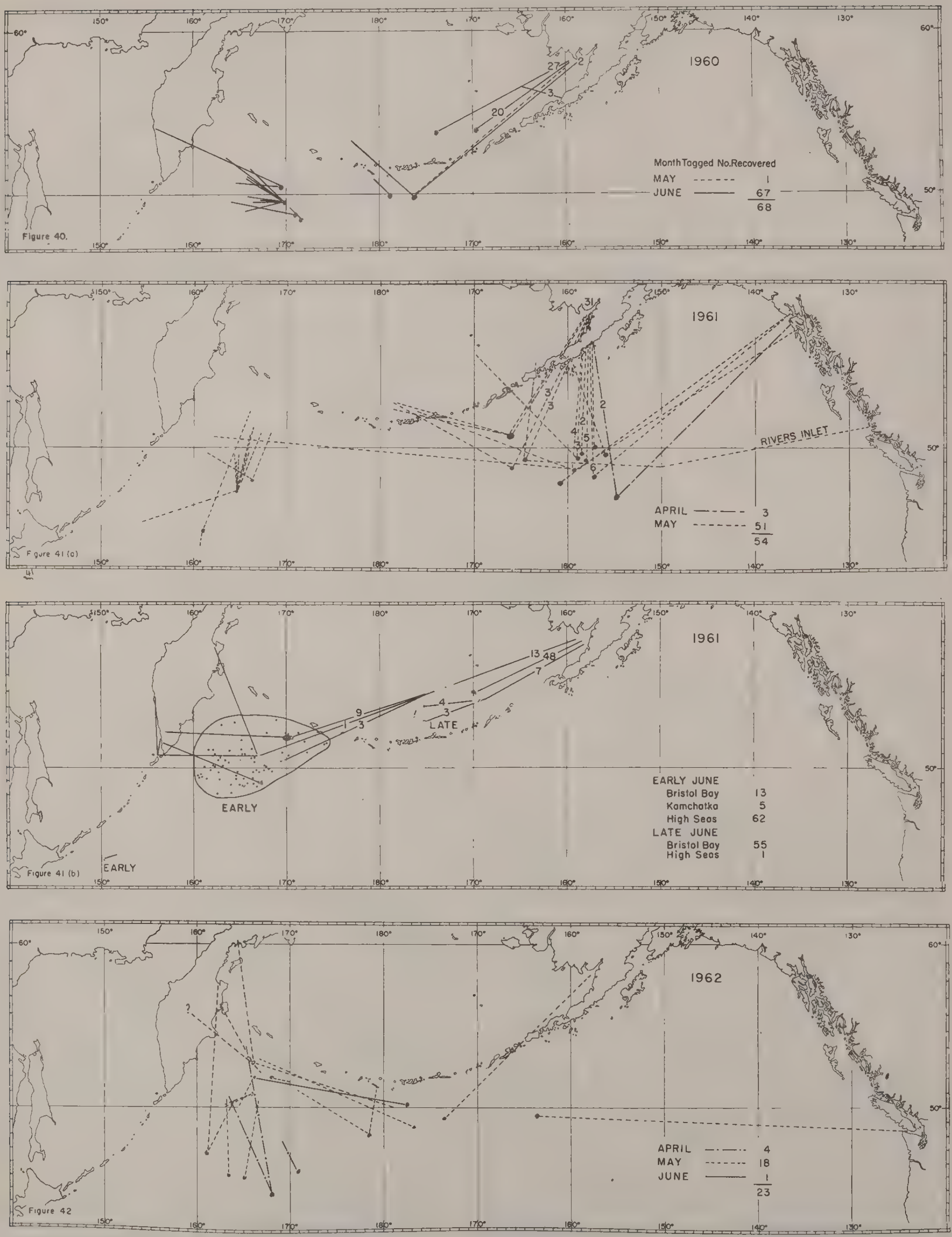


Figure 38.
1958
Month Tagged No. Recovered
JUNE 7
JULY 96
AUGUST 1
104
2
2
3
4
Figure 39.
1959
NASS RIVER
MAY 32
JUNE 23
JULY 8
63
3
150°
160°
170°
180°
170°
160°
150°
140°
130°
60°
50°

Figures 38–39. High seas and coastal recoveries of maturing sockeye salmon, Japanese tagging, 1958–59.


1960
27
2
3
20
Month Tagged No. Recovered
MAY ------ 1
JUNE ——— 67
68
Figure 40.
1961
31
3
3
2
4
2
5
3
6
RIVERS INLET
APRIL —·—·— 3
MAY ------ 51
54
Figure 41 (a)
1961
13
48
7
9
1
3
4
3
LATE
EARLY
EARLY JUNE
Bristol Bay 13
Kamchatka 5
High Seas 62
LATE JUNE
Bristol Bay 55
High Seas 1
EARLY
Figure 41 (b)
1962
?
APRIL —·—·— 4
MAY ------ 18
JUNE ——— 1
23
Figure 42
150°
160°
170°
180°
170°
160°
150°
140°
130°
60°
50°

FIGURES 40–42. High seas and coastal recoveries of maturing sockeye salmon, Japanese tagging, 1960–62.

tagging was done by the United States in the central, or central and western Aleutians, and when the Japanese fleet operated as far to the east as beyond 180° during either or both May and June. (See Hartt, 1962, 1966, for illustrations of the monthly disposition of the Japanese mothership fishery during 1956–60.)

In considering the above conclusion it should also be noted, by reference to Figures 31 to 37, firstly, that there have been no Kamchatkan coastal recoveries of maturing sockeye from the United States taggings and, secondly, that recoveries on the high seas north of the Aleutians did not extend westward beyond approximately 174°–175°E.

Besides the recoveries made in the Bering Sea there have been a number of recoveries south of the Aleutian Islands from taggings that were also conducted south of these islands. In almost all cases the fish had moved definitely in a westward direction, for either short or considerable distances. Some fish had moved somewhat southwards as well as to the west. It is not possible to be certain of the origin of these fish. Some could have been Bristol Bay sockeye, since the presence of Bristol Bay sockeye south of the Aleutians has been demonstrated by tagging as far west as 166°51′E. Others were almost undoubtedly of Kamchatkan origin, as may be confirmed by noting the pattern of recoveries from Japanese taggings in the waters west of the Aleutians (illustrated in Figures 38 to 42).

Japanese tagging, 1958–62. In some respects the high seas recoveries of sockeye tagged by Japan during 1958–62 are more difficult to interpret with respect to their origin since many must undoubtedly have been immature fish. Also, the Japanese taggings that provided high seas recoveries in these years covered a very broad area of ocean. They included taggings from far to the north in the Bering Sea to as far south in the North Pacific Ocean as approximately 43°N. They extended eastward in the North Pacific to as far as approximately 159°W.

Since the ocean distribution of the Japanese tagging operations varied considerably over the five years, it is perhaps best to discuss them briefly on an annual basis.

In 1958 (Fig. 38) there were two high seas recoveries from releases south of the mid-Aleutians (near 180°). Each of these fish had been tagged in June and each had travelled far to the west prior to recapture; therefore, they were probably of Kamchatkan origin.

The main Japanese taggings in 1958 were centered off southeastern Kamchatka in the approximate region of 51°N, 165°E. From these taggings there were many high seas recoveries which show a general pattern of progression towards the Kamchatka Peninsula and several actual recoveries in Kamchatkan coastal waters and streams. Probably there were some immature sockeye among these fish, but in the main they would appear to have been maturing Kamchatkan sockeye captured en route to the rivers of both east and west Kamchatka.

In 1959 (Fig. 39) there were six high seas recoveries in the Bering Sea, four from tagging in the Bering Sea, one from tagging south of Adak and one from tagging at approximately 48°N, 170°E. Age, length and gonad weight data indicate that these fish were maturing when tagged (Kondo *et al.*, 1965). From this information, together with knowledge of recovery dates and locations, it appears likely that the two fish tagged near 56°30′N, 175°E were destined for Kamchatka. The recovery locations of the other four fish are less revealing of their final destinations.

The remainder of the high seas recoveries in 1959 came from the taggings conducted south of 50°N, between 160°E and 170°E. Of the fish tagged in this general area approximately 90% were classified as maturing (Table 6 of INPFC, 1961, p. 65). The general pattern of recovery of these fish was mainly in a northwesterly direction towards the Kamchatka Peninsula, and there were two actual coastal recoveries, one on each coast. It is concluded, therefore, that these were mainly maturing Kamchatkan sockeye migrating towards the Kamchatka Peninsula. It is not possible to be more than speculative regarding the possible origin of recovered fish that had moved in either southerly or easterly directions.

High seas recoveries in 1960 (Fig. 40) included one in the Bering Sea (at roughly 53°30′N, 177°E) that had been tagged in June south of Adak near 50°N. This could have been a Bristol Bay sockeye, as could also the other that was tagged and recovered south of the Aleutians in the general area of 50°N, 180°.

The remaining high seas recoveries were from taggings conducted in the general area of 170°E between 48°N and 51°N, approximately. Of the 158 sockeye tagged here in June, 107 were classified as maturing (Appendix Table D of Kondo *et al.*, 1965). All but one of the 11 high seas recoveries had moved in a westerly direction. Thus it is concluded that these recoveries were predominantly maturing fish of Kamchatkan origin, intercepted in the course of their migration towards Kamchatka.

Tagging by Japan in 1961 extended as far east as into the Gulf of Alaska (Fig. 41). From these easternmost taggings there were five high seas recoveries in the Bering Sea east of 180° which, on the basis of size, time of tagging and recovery, and recovery location, were almost certainly maturing Bristol Bay

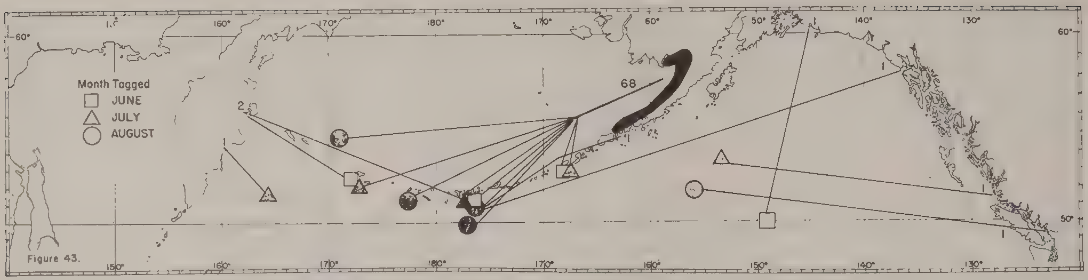


FIGURE 43. Coastal recoveries of sockeye salmon one year after tagging, 1956–61.

fish. In addition there was also one fish that had been tagged on May 9 at 48°29′N, 159°10′W that was recaptured on July 2 at 50°47′N, 162°29′E. This fish had a fork length of 55 cm when tagged and its age was 6_3. It was therefore almost certainly a maturing Kamchatkan sockeye.

From taggings during May in the general area to the southeast of the Kamchatka Peninsula, centered at about 165°E (Fig. 41a), there were nine fish recovered that showed distinctly northward movements, and one that had migrated in a northwesterly direction. In addition, two fish had moved southwards, one to the southwest and the other more directly southwards. The nine recovered fish that had migrated northwards probably included some Bristol Bay sockeye, since taggings in early June (Fig. 41b), in the area just north of that of the May taggings, provided 13 recoveries in Bristol Bay as well as several in Kamchatka, plus a number of high seas recoveries of fish which had moved predominantly towards the Kamchatka Peninsula and were undoubtedly mainly of Kamchatkan origin. However, it is also necessary to add that some of the recaptures from the early June taggings could have been immature fish.

In addition to the above there was one recovery in the Bering Sea from taggings conducted during late June just north of the Aleutian Islands, approximately at 176°W (Fig. 41b). This fish had moved a relatively short distance in an easterly direction. Its origin cannot be stated with any certainty, but it was a maturing male with a gonad weight at recapture of 30 grams (H. Kondo, personal communication).

The Japanese taggings in 1962 provided recoveries of fish that had moved in a variety of directions prior to recapture (Fig. 42). All but one of these had been tagged during April and May, the exception having been tagged in June. Since at the present time information on the maturity of these fish is incomplete, it is only tentatively concluded that those fish that had migrated distinctly towards the Kamchatkan coast were mainly Kamchatkan fish; the origin of the remainder is even more uncertain.

Recoveries of Fish Tagged as Immatures

Coastal recoveries one year after tagging. The coastal recoveries of immature sockeye salmon one year after tagging, from taggings by Japan, the United States and Canada during the years 1956–61 are illustrated in Figure 43.

During this period recoveries to western Alaska totalled 68. Two of these had been tagged in the Bering Sea, at approximately 171°E (at 55°N). The remaining recoveries to western Alaska were tagged relatively close to the southern shores of the Aleutian

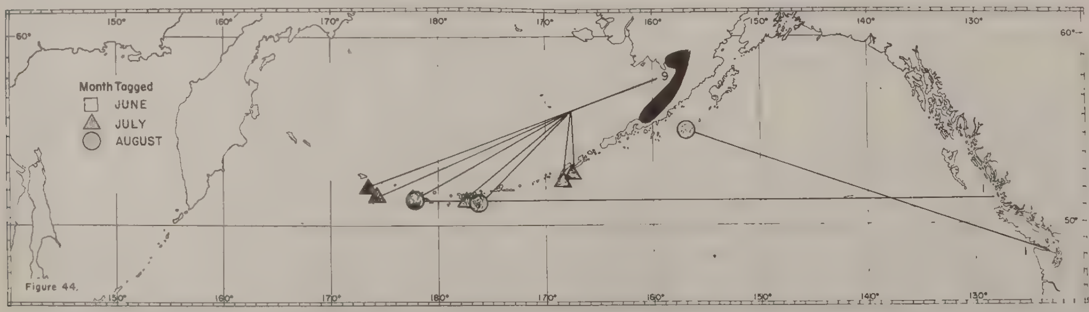


FIGURE 44. Coastal recoveries of sockeye salmon two years after tagging, 1956–60.

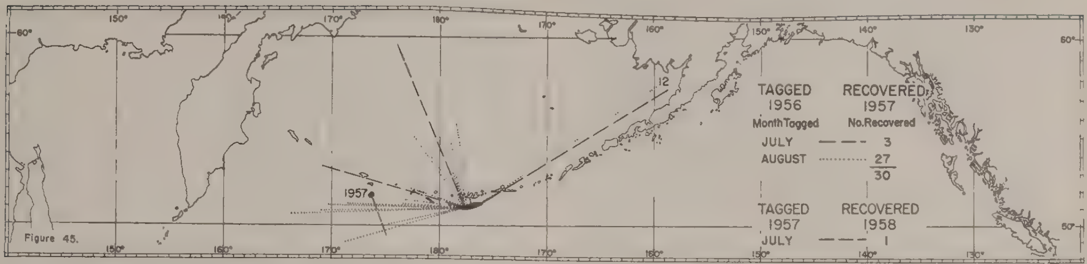


Figure 45.
TAGGED 1956
RECOVERED 1957
Month Tagged
No. Recovered
JULY 3
AUGUST 27
30
TAGGED 1957
RECOVERED 1958
JULY 1
1957
12
150°
160°
170°
180°
140°
130°
60°
50°

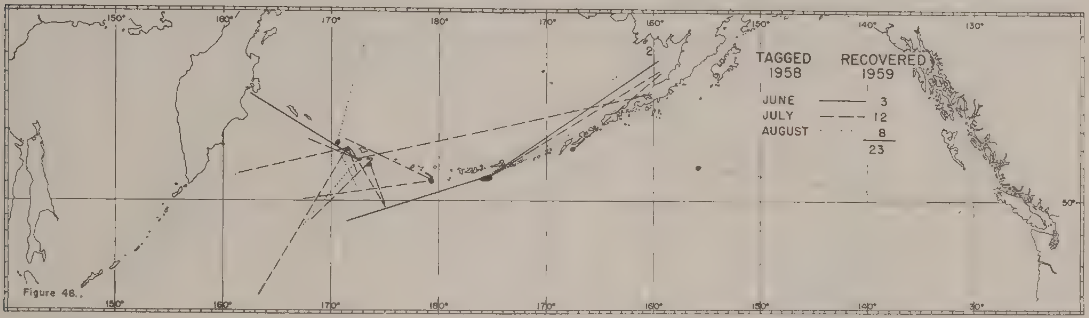


Figure 46.
TAGGED 1958
RECOVERED 1959
JUNE 3
JULY 12
AUGUST 8
23
2
150°
160°
170°
180°
140°
130°
50°

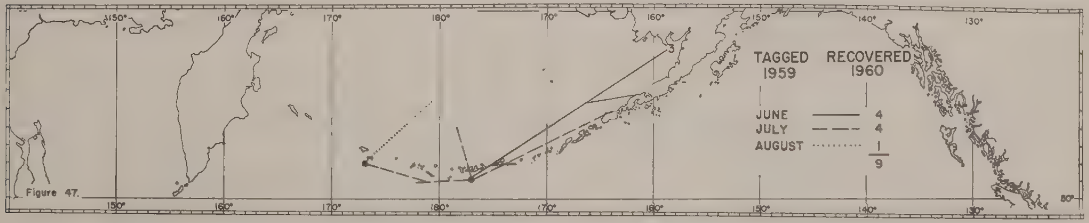


Figure 47.
TAGGED 1959
RECOVERED 1960
JUNE 4
JULY 4
AUGUST 1
9
3
150°
160°
170°
180°
140°
130°
50°

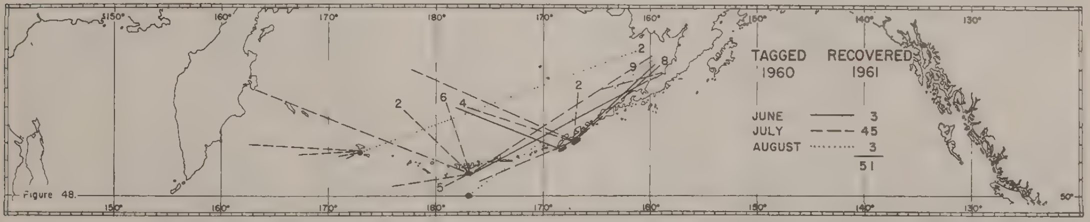


Figure 48.
TAGGED 1960
RECOVERED 1961
JUNE 3
JULY 45
AUGUST 3
51
2
9
8
2
2
6
4
5
150°
160°
170°
180°
140°
130°
50°

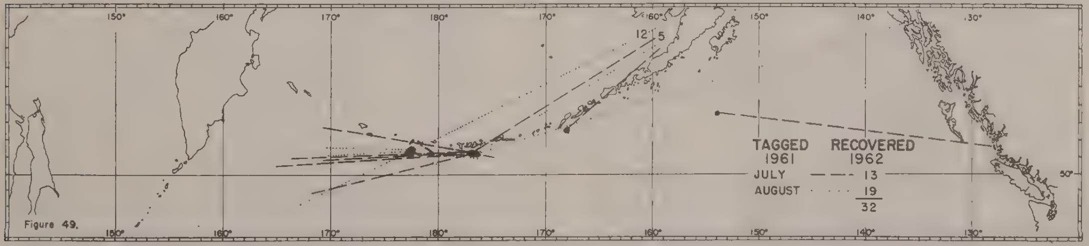


Figure 49.
TAGGED 1961
RECOVERED 1962
JULY 13
AUGUST 19
32
12
5
150°
160°
170°
180°
140°
130°
50°

FIGURES 45–49. High seas and coastal recoveries of sockeye salmon one year after tagging, United States tagging, 1956–61.

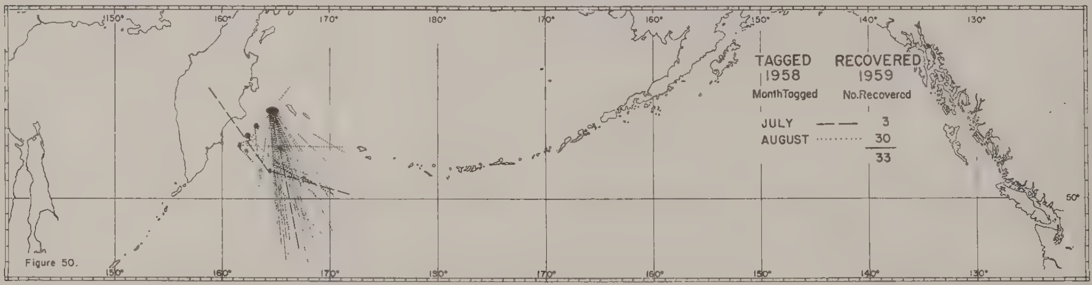
Islands, from about 172°E in the west to about 167°W in the east.

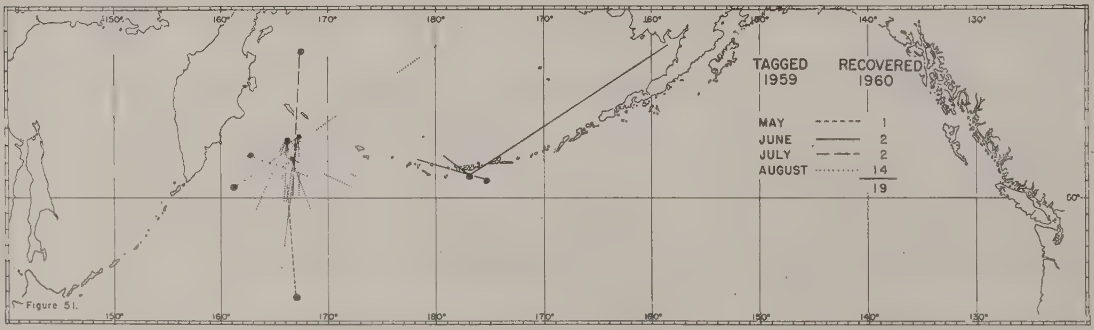
There have been three recoveries to Kamchatka during this period (two to the Kamchatka River and one to an unknown locality), the easternmost tagging location of these fish being almost directly south of and close to Adak Island, at about 176°30′W.

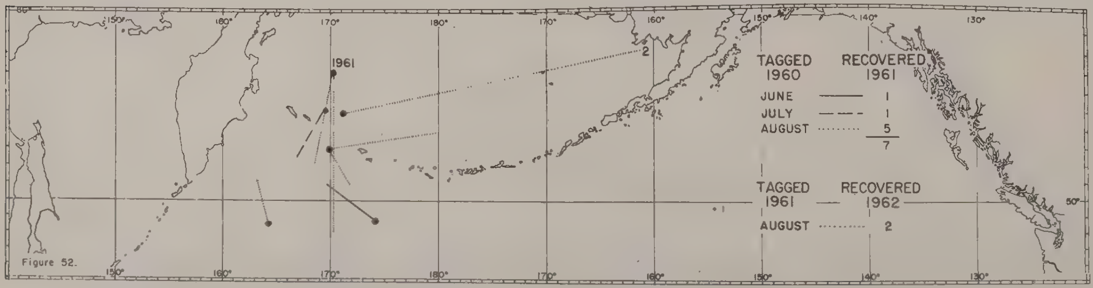
The remaining recoveries include one to the southern tip of the Alaska Peninsula, and one each to the Copper River, southeastern Alaska, Rivers Inlet and the Fraser River. The tagging locations can be seen in Figure 43. Of particular interest is the recovery in southeastern Alaska of a fish which was tagged as far west as about 176°30′W, just south of Adak.

It may also be noted that there were no recoveries from taggings farther south than 50°N, even though considerable taggings were conducted by the three countries during this period in more southerly waters (Figs. 5 to 19).

Coastal recoveries two years after tagging. These recoveries are illustrated in Figure 44. From the 1956–60 tagging operations by the three countries there have been nine such recoveries to western Alaska, none to any Asian territory, one to Rivers Inlet and one to Puget Sound. The western Alaskan recoveries were all of fish tagged south of and close to the Aleutian Islands, from approximately 173°30′E in the west to approximately 168°30′W in the east. The Rivers Inlet recovery had been tagged as far to the west as 177°30′E, close to the southern shores of the islands in that region. This recovery represents the farthest known western limit of distribution of sockeye salmon


150°
160°
170°
180°
170°
160°
150°
140°
130°
TAGGED 1958
RECOVERED 1959
Month Tagged
No. Recovered
JULY 3
AUGUST 30
33
50°
Figure 50.


150°
160°
170°
180°
170°
160°
150°
140°
130°
TAGGED 1959
RECOVERED 1960
MAY 1
JUNE 2
JULY 2
AUGUST 14
19
50°
Figure 51.


150°
160°
170°
180°
170°
160°
150°
140°
130°
1961
2
TAGGED 1960
RECOVERED 1961
JUNE 1
JULY 1
AUGUST 5
7
TAGGED 1961
RECOVERED 1962
AUGUST 2
50°
Figure 52.

Figures 50–52. High seas and coastal recoveries of sockeye salmon one year after tagging, Japanese tagging, 1958–61.

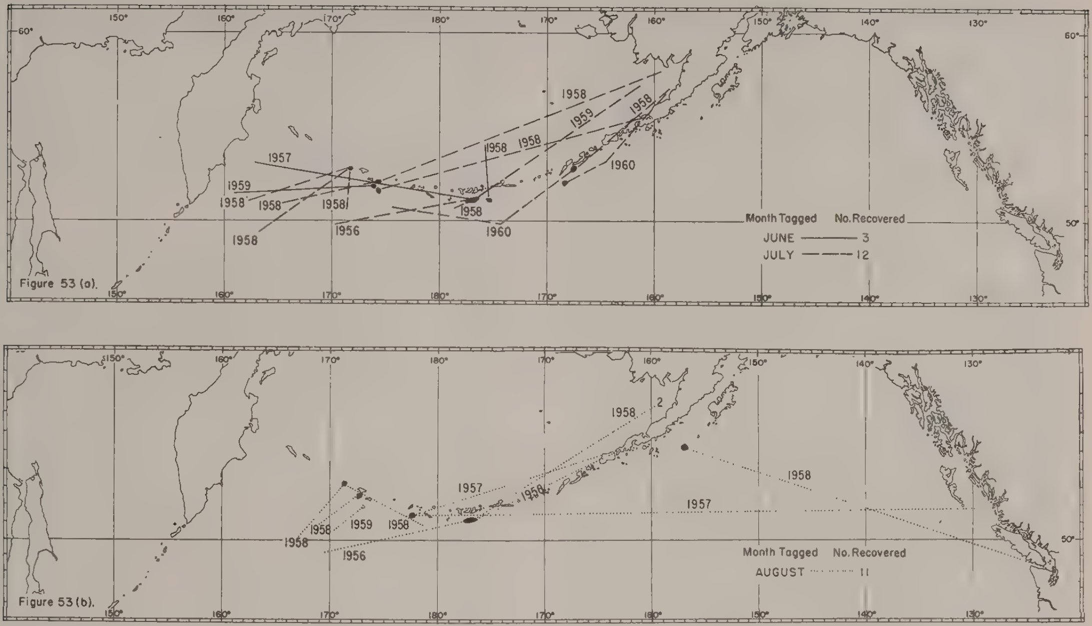


FIGURE 53. High seas and coastal recoveries of sockeye salmon two years after tagging, Japanese and United States tagging, 1956–60.

originating in territory of the Gulf of Alaska or farther south.

High seas recoveries. The high seas recoveries of sockeye salmon tagged as immatures and recovered one or two years after tagging are shown in Figures 45 to 53 (the coastal recoveries, which have already been described, are also shown in these illustrations). The interpretation of these recoveries in relation to their probable continent of origin is complex and difficult, because certain specific factors pertaining to each individual fish must first be known and considered. In particular, there should be certainty regarding their maturity when recaptured, as it is only with the maturing individuals that reliable conjectures can be made regarding their probable coastal destination. The origin of those that were recovered while still immature is impossible to determine with any useful degree of certainty, because, as the data already presented have indicated, there can be intermingling between immature fish of the two continents.

Determination of the maturity of recaptured individuals can be made fairly reliably from information on their age, size, and location and date of recovery. However, such detailed information cannot properly be dealt with here, nor, frequently, are such data yet available. The reader is referred to Hartt (1962, 1966) and Kondo *et al.* (1965) for detailed analyses of recoveries of sockeye tagged as immatures by the United States and Japan, respectively. Here, discussion will be limited to a brief summary of the significance of this type of recovery, either in relation to continental origin when possible, or in other respects, such as the information they provide regarding the oceanic dispersal of sockeye salmon during the course of their sojourn in the sea.

Dealing first with United States taggings, reference is made to Figures 45–49 which illustrate the recoveries made one year after tagging for the years 1956–61. During these years it is probable that most of the fish recovered in the Bering Sea were of western Alaskan origin (Hartt, 1962, 1966). This conclusion is based on knowledge that most of these fish were maturing when recaptured, on the fact that from the same taggings there were a number of recaptures actually within Bristol Bay or its surroundings, and from the detailed information already gained from seining operations and from the tagging and recovery of maturing sockeye salmon regarding the timing and the routes by which western Alaskan sockeye return to that area.

The continental origin of those fish that were recovered in the North Pacific Ocean, either close to the Aleutians or farther south, is not possible to determine with any sufficient degree of certainty. Detailed examination of the data (i.e., age, size, and time and location of recovery) suggests that some of these fish were maturing when recaptured and that they probably included fish of both Kamchatkan and western Alaskan origin. In any event, they do not extend the limits of eastern or western distribution of Kamchatkan or western Alaskan sockeye, respectively, as already determined from coastal recoveries. It should also be noted that whereas some of the recoveries were made close to the Aleutians, where the fish had first been captured, many others occurred either much farther to the west or well to the south, or both.

Recoveries one year after tagging of sockeye tagged by Japan as immatures are shown in Figures 50–52. Again, data on maturity at recapture are needed to be able to make reasonable interpretations regarding probable continent of origin, and for the most part such data are not presently available. On the basis of coastal recoveries of maturing fish made from taggings close to where some of these fish tagged as immatures were recaptured, it is almost certain that they included some maturing fish of Kamchatkan origin. However, it is also possible that western Alaskan fish were included, as evidenced by the fact that tagging by Japan in early June of 1961 in the general area between 167°E and 170°E and north of 50°N provided a number of recoveries of maturing fish in Bristol Bay (Fig. 41b).

These many recoveries one (Figs. 45 to 52) or two (Fig. 53) years after tagging, from operations by both Japan and the United States, provide information on the oceanic dispersal of immature sockeye during the winter months. The seining and recovery data previously described have shown that immature sockeye are present in the " westward stream " south of the Aleutians and that others move northward towards the Kamchatka Peninsula from the southeast. The numerous recoveries of sockeye one or two years after tagging at locations well to the south of where they were tagged point to the fact that the northward migrations during the summer must be followed at a later date by migrations to the south. Thus these data support an hypothesis that many immature sockeye salmon from both Kamchatka and western Alaska winter in the warmer, more southerly waters of the North Pacific.

In conclusion, it should also be noted that some of these immature fish repeated their migration past a given location at least twice and perhaps three times during their sojourn in the sea (for example, past Adak, as described by Hartt, 1966). As Hartt suggests, it would therefore seem possible " that salmon at sea may follow a course that is repeated cyclically, perhaps annually ". It is therefore credible, as has been shown for sockeye smolts (Johnson and Groot, 1963), that salmon at sea possess an " internal clock or diurnal rhythmic sense that allows fish to make the proper adjustments to the diurnally and seasonally changing phenomena ".

Area and Extent of Intermingling

Maturing Kamchatkan and western Alaskan sockeye. The positively known area and extent of intermingling between maturing Kamchatkan and western Alaskan sockeye, determined by tagging, is based upon the coastal recoveries illustrated in Figures 19, 20 and 21.

Recoveries from west and east Kamchatka from taggings by Japan, Canada and the United States up to and including 1962 have amounted to only 10 from west Kamchakta (Fig. 19) and 12 from east Kamchatka (Fig. 20). In addition, there was one recovery in 1962 from an unspecified area in Kamchatka. All but one of these fish had been tagged in the western North Pacific, to the southeast of the Kamchatka Peninsula. The exception had been tagged in the western Bering Sea, relatively close to the mid-central coast of east Kamchatka.

The eastern limit of capture of these Kamchatkan coastal recoveries occurred just south of the western Aleutian island, Agattu, at approximately 173°30′E (51°30′N). This fish was tagged by Japan in June of 1938, and was recovered in a coastal fishery near the Kuril Strait. The southern limit is defined by the recovery in east Kamchatka of a fish tagged by Japan in May of 1962 at approximately 47°N, 161°E.

All these recoveries have come from taggings by Japan. There have been no Asian coastal recoveries from any taggings by either the United States or Canada, up to and including 1962.

There have been numerous recoveries up to 1962 of maturing sockeye in western Alaska. In the North Pacific Ocean the tagging locations of such recoveries have extended from as far to the west as approximately 167°E (at 51°N) to as far east into the Gulf of Alaska as 142°30′W (at about 56°N). The southern limit is defined by two recoveries of fish tagged within the Gulf of Alaska at 46°N (at 155°W). The western, and also the northern, limit in the Bering Sea is represented by a single recovery of a fish tagged at approximately 58°N, 176°E. With one exception, the remainder of the many recoveries from taggings in the Bering Sea came from releases made to the east of 180°. The exception was tagged close to the Aleutian Islands at about 177°E (52°30′N).

Based only on coastal recoveries, then, the ocean distributions of maturing Kamchatkan and western Alaskan sockeye have been shown to overlap in the North Pacific Ocean between 50°N and the Aleutian Islands, from 167°E to 173°30′E.

In considering the above it should be realized that the term "overlapping" does not necessarily infer "intermingling" between Kamchatkan and western Alaskan sockeye. The latter term implies the occurrence at the same time and at the same place of fish of different stocks. The extent of overlapping that is described above was based on taggings made in different years. In actual fact, it was only in 1961 that recoveries were made to both Kamchatka and western Alaska from taggings conducted within the area of overlap at roughly the same time. These recoveries indicated actual intermingling between Kamchatkan and western Alaskan sockeye during early June 1961 in the area between 50°N and 52°N from 167°E to approximately 171°E.

Further information on intermingling between maturing Kamchatkan and western Alaskan sockeye is provided by the recoveries of tagged fish made on the high seas. With a few exceptions all these recoveries were made by vessels of the Japanese mothership fishery. They are illustrated in Figures 31 to 42.

As explained in an earlier section, provided the maturity of these fish is established, it is possible to be fairly certain of the continental origin of most of them, based on knowledge regarding the timing and direction of movement of concentrations of sockeye towards Kamchatka and western Alaska, and because these recoveries form series or patterns that are consistent with the recoveries that were actually made in coastal waters.

In the section titled "High seas recoveries of maturing sockeye", it was concluded that most of the high seas recoveries made in the Bering Sea, from taggings mainly south of the Aleutians but also from taggings within the Bering Sea, were fish of western Alaskan origin. These do not extend the known western limit of distribution of maturing western Alaskan sockeye beyond those already determined from actual coastal recoveries. However, if consideration is given to the annual and seasonal dispersal of the Japanese mothership fishery in the Bering Sea in relation to tag recoveries, and to the fact that there have been no Kamchatkan coastal recoveries either from any taggings in the North Pacific at least as far west as Attu Island or from any taggings within the Bering Sea itself, these recoveries indicate that at least in some years (1960, 1961) maturing western Alaskan sockeye predominated in the Bering Sea, possibly as far west as about 175°E.

A few recoveries in the Bering Sea may have been fish of Kamchatkan origin, because of the fact that after being tagged in the Bering Sea they had moved in a distinctly westward direction. However, it is not possible to be certain of this.

The high seas recoveries from taggings by Japan and the United States south of the Aleutian Islands do not extend the western limit of distribution of western Alaskan sockeye beyond that determined on the basis of actual coastal recoveries—at approximately 167°E, near 50°N (in June 1961; Fig. 41b). There is no evidence to indicate that western Alaskan sockeye were predominant that far to the west in that particular year and time. However, if allowance is made for paucity of tagging in adequate numbers at appropriate times and places, and considering that some, possibly many, of the fish recaptured on the high seas were immature, then the 1956–62 recoveries strongly suggest that in some years western Alaskan sockeye predominated at least to almost 175°E south of the Aleutians (Fig. 35b) and were relatively abundant even farther west, at least to almost 169°E (Fig. 41b, and see also Figs. 32 and 33).

There have been a large number of high seas recoveries, primarily from Japanese taggings during 1958–62, which almost certainly must have included many maturing sockeye of Kamchatkan origin. The taggings referred to are those that were made each year in the 1958–62 period between the meridians of 160°E and 170°E, from about 52°N south to about 43°N. This conclusion is based on the facts that sampling indicated that most of the fish being tagged were maturing sockeye (see section titled "High seas recoveries of maturing sockeye"), that the distribution of recoveries was progressively in a northwesterly direction towards the Kamchatkan coast, and that these same taggings provided a number of recoveries from east and west Kamchatka (Figs. 38 to 42).

In themselves these particular recoveries do not extend the eastern limit of occurrence of maturing Kamchatkan sockeye in the North Pacific beyond that already determined on the basis of coastal recoveries as described above. However, in addition to these there have been a number of recoveries from taggings south of the Aleutians which almost certainly do so, particularly those shown in Figure 32 (one tagged just west of 180° at about 51°N), Figure 38 (two tagged near 180° north of 50°N), Figure 42 (two tagged at about 177°W, one near 49°N and one near 50°N) and Figure 41a (of special significance, one tagged as far to the east as 159°W, at 48°30′N, and recovered at approximately 51°N, 162°E). As was mentioned in an earlier section, it is almost certain that this latter recovery was of a maturing Kamchatkan fish, since it was recovered so close to the Kamchatkan coast as late as July 2, and because of its size (fork length 55 cm) and age (6_3) at tagging.

The conclusion to be drawn from a consideration of high seas recoveries regarding the distribution of maturing Kamchatkan sockeye in the North Pacific Ocean is that they may be present as far to the east as 159°W and that they predominate among the concentrations of maturing sockeye found off the southeast coast of Kamchatka at least as far east as 170°E.

Tagging has not provided any positive evidence regarding the limits of distribution, or the region of predominance, of maturing Kamchatkan sockeye in the Bering Sea.

Immature Kamchatkan and western Alaskan sockeye. The coastal recoveries of sockeye tagged as immatures and recovered as maturing fish one or two years later, from taggings by the United States, Japan and Canada up to and including 1961, are summarized and illustrated in Figures 43 and 44.

These show the presence in the Bering Sea of immature western Alaskan sockeye as far west as approximately 171°E (at about 55°N).

Immature western Alaskan sockeye were found south of and close to the Aleutians from near Attu Island in the west (at about 172°E) to Unalaska Island in the east (at about 167°30′W).

There have been no recoveries in Asian coastal waters of immature sockeye tagged in the Bering Sea. From taggings south of and close to the Aleutians there was a recovery from east Kamchatka (tagged at approximately 176°30′W).

Thus a region of overlapping between Kamchatkan and western Alaskan immature sockeye occurred between 172°E and 176°30′W directly south of the Aleutians. There was intermingling between the two groups of fish close to the Aleutian Islands at 176°–177°W in 1960, since in that year taggings at approximately the same time and in the same location gave 10 returns from western Alaska and one from east Kamchatka.

The significance of the high seas recoveries of sockeye tagged as immatures, in relation to continental origin, has been discussed in the section titled "Recoveries of fish tagged as immatures". It was concluded that probably most of the recoveries made in the Bering Sea were fish of western Alaskan origin, that recoveries made south of the Aleutians could have included fish of both continents, and that the high seas recoveries in any event did not extend the eastern and western limits of distribution of Kamchatkan and western Alaskan fish, respectively, beyond those already determined on the basis of coastal recoveries.

In summary, then, the recoveries one or two years later of sockeye salmon that were tagged when they were immature fish have given some indication of the oceanic distribution of immature sockeye. They would appear to be at least as widely dispersed as the maturing sockeye, at comparable periods of time. Also, there is evidence that fish from the two continents intermingle in certain oceanic areas during some period of the year at least. However, it is difficult to define with any certainty the limits of areas where fish from either continent might be predominant. On the basis of coastal recoveries, it would appear certain that western Alaskan immature sockeye predominate among the concentrations that migrate westward along the south side of the Aleutian Chain to at least as far west as 180°, and possibly even farther west in some years (1960, 1961). Less can be said in this connection about Kamchatkan sockeye, mainly because of the paucity of coastal recoveries (only three). However, the high seas recoveries suggest that the main concentrations of immature Kamchatkan sockeye approach the Kamchatka Peninsula from the southeast rather than from more directly eastward

TABLE 6. Limits of distribution of principal sockeye salmon stocks originating in Gulf of Alaska territory (including the Columbia River).

Stock	Numbers recovered (up to 1962)	Northern limit	Southern limit	Eastern limit	Western limit
Chignik R. area	28	—	48°N	137°30′W	168°W
Kodiak I.	89	58°30′N	46°N	138°W	176°30′W
Cook Inlet	76	—	50°N	141°30′W	168°W
Copper R.	77	—	53°N	137°W	154°W
Southeastern Alaska	73	59°N	46°30′N	—	161°W
Nass-Skeena area	105	58°N	51°N	—	177°W
Central B. C.	32	57°30′N	50°N	—	154°W
Rivers-Smith inlets	73	57°N	47°N	—	164°30′W
Fraser R.	163	58°N	46°30′N	—	163°30′W
Columbia R.	4	50°N	47°N	—	153°W

along the Aleutian Chain, so that they are probably predominant in waters at least from 170°E westward.

Sockeye in the Gulf of Alaska. Taggings in the Gulf of Alaska (Figs. 21 to 30), particularly in 1961 and 1962, have shown that maturing sockeye from Bristol Bay southwards to the Columbia River intermingle over a broad area of the Gulf. The limits of distribution of the principal stocks originating in Gulf of Alaska territory (and including the Columbia River) are given in Table 6.

Table 6, and the illustrations cited, show that individuals of some stocks were found far to the west outside of the Gulf of Alaska. Most of these had been tagged close to the Aleutian Islands, but there have been no recoveries in the Gulf of any sockeye tagged within the Bering Sea.

In addition to these, there have been a number of coastal recoveries of sockeye originating in areas bordering the Gulf of Alaska which were tagged as immatures. These were as follows:

Year and location of tagging	*Year and location of recovery*
1957, 52°N, 177°30′E	1959, Rivers Inlet, B.C.
1958, 55°30′N, 157°W	1960, Puget Sound
1958, 52°N, 156°W	1959, Fraser River
1961, 51°N, 177°W	1962, southeastern Alaska
1961, 53°30′ [illegible]	[illegible]2 Rivers Inlet
1961, 50° [illegible] W	[illegible]2, Copper River

Evidence from Parasitology

An extensive survey and analysis of the distribution of the parasites of sockeye salmon, to ascertain their use as indicators of the origin of their hosts, was carried out by Canadian investigators (INPFC, 1956 to 1961; Margolis, 1963). Mamaev *et al.* (1959) reported on a preliminary study having the same objective. Their samples were restricted in number and distribution, and the results were inconclusive. They examined 122 adults and 34 pre-downstream migrant sockeye from five Kamchatkan localities and 27 sockeye from the North Pacific off the east coast of Kamchatka. Parasitological studies were also conducted by Japan, but were limited to the identification of the parasites found in a small number of sockeye taken on the high seas, and did not provide information relevant to the problem of identifying the origins of the fish (INPFC, 1957 and 1959; Fukui, 1960 and 1961).

The Canadian studies, involving examinations of almost 13,000 sockeye, were restricted almost entirely to metazoan parasites (helminths and copepods). The search for protozoa was not given exhaustive treatment. Between 50 and 60 species of parasites were found. Initially, several marine and freshwater parasites were proposed as possible indicators of the origin of sockeye (INPFC, 1957). However, the results of further and more extensive sampling revealed that some of the initially selected "possible indicator species" were not useful (INPFC, 1958 and 1959) and that the value of two marine trematodes, *Hemiurus levinseni* and *Tubulovesicula lindbergi*, was not entirely clear (INPFC, 1960). The distribution of sockeye infected with these two trematodes suggests that *H. levinseni* is primarily associated with sockeye of Asian origin and that *T. lindbergi* is primarily associated with sockeye of North American origin, although it is apparent that neither of these parasites can be used to identify the origin of individual fish. A lack of knowledge of certain aspects of their biology, particularly their life spans in sockeye, prevented a satisfactory assessment of their value in indicating the oceanic distribution of Asian and North American stocks of sockeye (Margolis, 1963).

From the total array of parasites that were found in sockeye, two species of freshwater origin were finally selected as useful in providing evidence of the origin of their hosts. These are the cestode *Triaenophorus crassus* (plerocercoid larval stage in the body musculature), found only in sockeye of western Alaskan (essentially Bristol Bay) origin, and the intestinal nematode *Dacnitis truttae*, found only in sockeye of Kamchatkan origin. No parasites fulfilling the role of "natural tags" were found in the sockeye stocks originating in the river systems tributary to the Gulf of Alaska and the northeast Pacific Ocean.

Because samples from Kamchatkan rivers were generally unavailable, the overall rates of *Dacnitis* infection in the samples of maturing sockeye from the North Pacific westward from 175°E give the best indication of the incidence of *Dacnitis* in Kamchatkan sockeye as a whole. These rates of infection (Table 7) suggest that generally about 1% to 2% (perhaps less than 1% in some years, as indicated in 1959) of Kamchatkan sockeye are infected with *Dacnitis*. The Okhotsk Sea samples (Table 7), taken off the southwest coast of Kamchatka, showed a higher rate of *Dacnitis* infection (average annual rate for samples taken from 1955 to 1958 varied from 2% to 10%), but these samples cannot be considered as reflecting the overall incidence in Kamchatkan sockeye, nor even in west Kamchatkan sockeye. As will be discussed in the following section on morphology, the age composition of the Okhotsk Sea samples suggests that they do not represent the principal west Kamchatkan stock (i.e., Ozernaia River sockeye) but rather that they consist of fish from minor runs. The single sample available from the Ozernaia River in 1959 (Table 7) indicates that *Dacnitis* was either absent or extremely scarce in sockeye from that river. The estimated overall rate of *Triaenophorus* infection in

TABLE 7. Frequency of *Dacnitis* in maturing sockeye salmon from areas where all or the vast majority probably were of Kamchatkan origin[1].

Sampling period	Okhotsk Sea			North Pacific (W from 175°E)			Bering Sea (W from 175°E)[2]			Ozernaia River		
	No. examined	Infected No.	Infected %	No. examined	Infected No.	Infected %	No. examined	Infected No.	Infected %	No. examined	Infected No.	Infected %
1955												
May–June	5	1	20	50	1	2	—	—	—	—	—	—
July–August	20	1	5	25	0	0	—	—	—	—	—	—
Total	25	2	8	75	1	1.3	—	—	—	—	—	—
1956												
May–June	25	2	8	14	0	0	—	—	—	—	—	—
July–August	25	3	12	42	1	2.4	—	—	—	—	—	—
Total	50	5	10	56	1	1.8	—	—	—	—	—	—
1957												
May–June	25	0	0	106	2	1.9	25	1	4	—	—	—
July–August	50	3	6	94	1	1.1	41	0	0	—	—	—
Total	75	3	4	200	3	1.5	66	1	1.5	—	—	—
1958												
May–June	50	1	2	486	6	1.2	110	1	0.9	—	—	—
July–August	50	1	2	164	2	1.2	5	0	0	—	—	—
Total	100	2	2	650	8	1.2	115	1	0.9	—	—	—
1959												
May–June	—	—	—	338	2	0.6	—	—	—	—	—	—
July–August	—	—	—	24	0	0	—	—	—	126[3]	0	0
Total	—	—	—	362	2	0.55	—	—	—	126	0	0

[1] Based on data given in Margolis (1963).

[2] The Bering Sea samples westward from 175°E in 1959 are not included because the rates of *Triaenophorus* infection suggested that a substantial (although not dominant) proportion of them were of Bristol Bay origin.

[3] Sampling date was actually September 1.

Bristol Bay sockeye showed annual variations between 3.2% and 22% in the years 1957 to 1959 (1957, 3.2%; 1958, 22.0%; 1959, 10.6–13.3%; see Tables XXII, XXIII and XXIV of Margolis, 1963). Thus, *T. crassus* occurs more frequently in Bristol Bay sockeye than does *D. truttae* in Kamchatkan sockeye and consequently the former parasite is probably more useful in determining the oceanic distribution of Bristol Bay sockeye than is the latter in establishing the distribution of Kamchatkan sockeye. Also, the value of *D.*

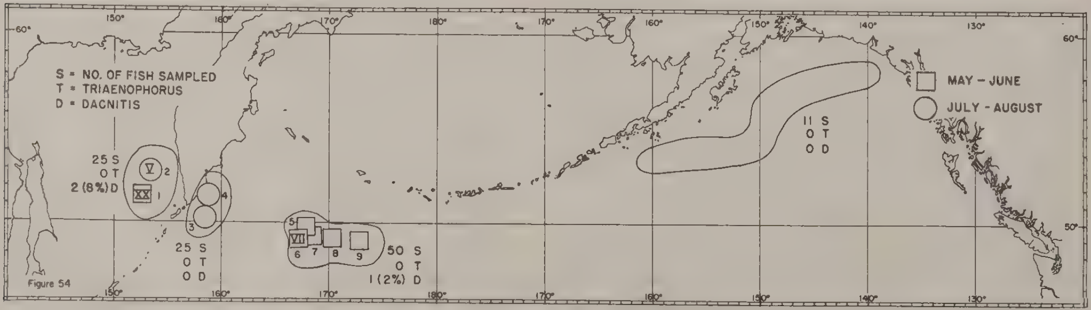


FIGURE 54. Incidence of *Dacnitis* in high seas samples of maturing sockeye salmon in 1955. (No *Triaenophorus*-infected sockeye were found.) Samples from the Gulf of Alaska (July–August) consisted of only one or two fish each and their locations are not shown individually. Roman numerals represent percent infection with *Dacnitis*. Small numerals outside the circles are station numbers as given in Table XII of Margolis (1963). (From Margolis, 1963.)

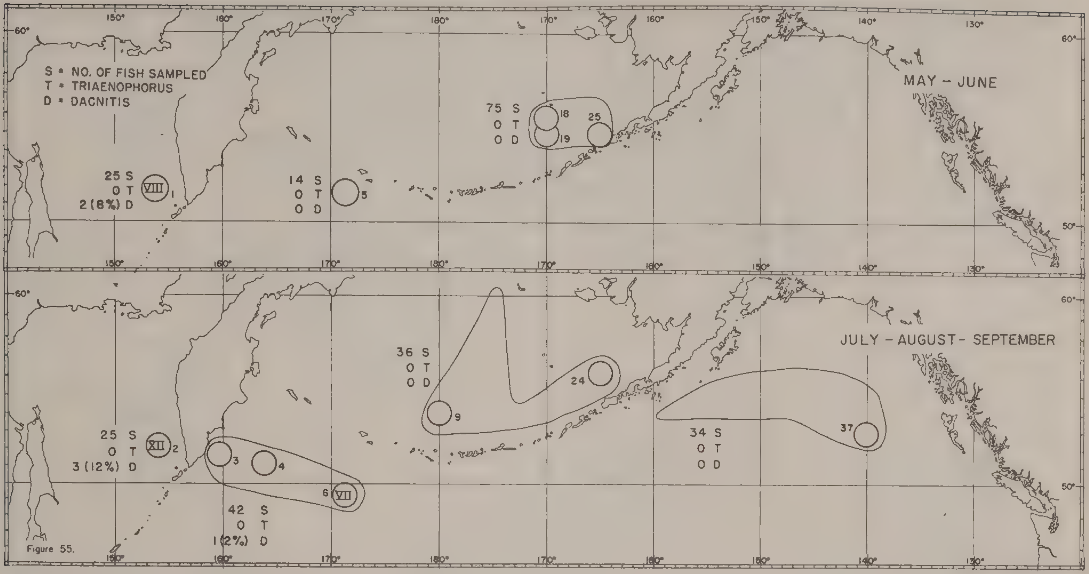

S = NO. OF FISH SAMPLED
T = TRIAENOPHORUS
D = DACNITIS
MAY – JUNE
25 S
0 T
2 (8%) D
VIII
1
14 S
0 T
0 D
5
75 S
0 T
0 D
18
19
25
JULY – AUGUST – SEPTEMBER
36 S
0 T
0 D
9
24
25 S
0 T
3 (12%) D
XII
2
3
4
6
VII
42 S
0 T
1 (2%) D
34 S
0 T
0 D
37
Figure 55.
150°
160°
170°
180°
170°
160°
150°
140°
130°
60°
50°

Figure 55. Incidence of *Dacnitis* in high seas samples of maturing sockeye salmon in 1956. (No *Triaenophorus*-infected sockeye were found.) Samples of less than 9 sockeye are not shown individually. Roman and Arabic numerals have the same significance as in Figure 54, except that station numbers are as given in Table XIII of Margolis (1963). (From Margolis, 1963.)

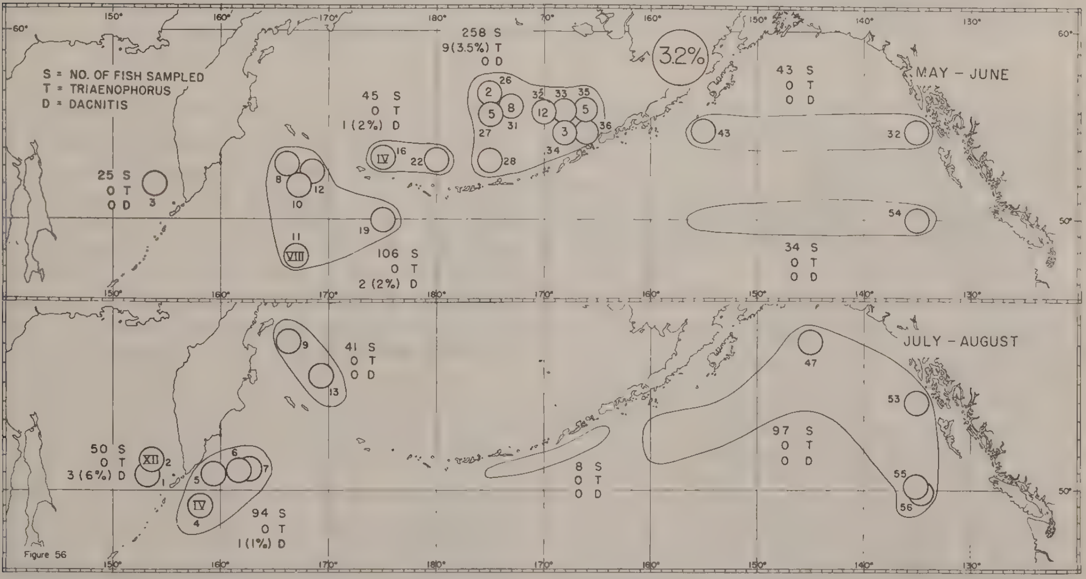

S = NO. OF FISH SAMPLED
T = TRIAENOPHORUS
D = DACNITIS
MAY – JUNE
258 S
9 (3.5%) T
0 D
3.2%
43 S
0 T
0 D
45 S
0 T
1 (2%) D
IV
16
22
2
26
5
8
31
27
28
32
33
35
12
5
3
36
34
43
32
25 S
0 T
0 D
3
8
12
10
19
11
VIII
106 S
0 T
2 (2%) D
54
34 S
0 T
0 D
JULY – AUGUST
41 S
0 T
0 D
9
13
47
53
50 S
0 T
3 (6%) D
XII
2
1
5
6
7
IV
4
94 S
0 T
1 (1%) D
8 S
0 T
0 D
97 S
0 T
0 D
55
56
Figure 56
150°
160°
170°
180°
170°
160°
150°
140°
130°
60°
50°

Figure 56. Incidence of *Triaenophorus* and *Dacnitis* in high seas samples of maturing sockeye salmon in 1957. Samples of less than 12 sockeye are not shown individually. Roman and Arabic numerals within the circles represent percent infection with *Dacnitis* and *Triaenophorus*, respectively. Small numerals outside the circles are station numbers as given in Table XIV of Margolis (1963). (From Margolis, 1963, modified in the May–June chart to show the estimated overall rate of *Triaenophorus* infection in Bristol Bay adults, for comparison with high seas rates of infection.)

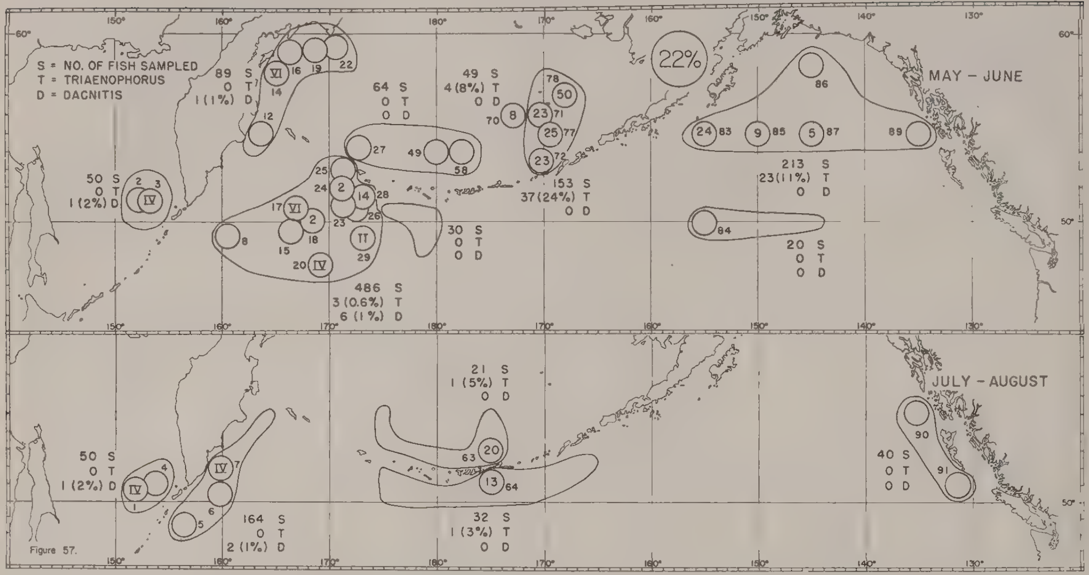


FIGURE 57. Incidence of *Triaenophorus* and *Dacnitis* in high seas samples of maturing sockeye salmon in 1958. Samples of less than 10 sockeye are not shown individually, except at Station 28 (7 fish), Station 63 (5 fish), Station 64 (8 fish) and Station 78 (2 fish). Roman and Arabic numerals have the same significance as in Figure 56, except that station numbers are as given in Table XV of Margolis (1963). (From Margolis, 1963, modified in the May–June chart to show the estimated overall rate of *Triaenophorus* infection in Bristol Bay adults, for comparison with high seas rates of infection.)

truttae is impaired because it was not possible, due to lack of samples, to determine the extent of its distribution in Kamchatkan stocks and the rates of infection in individual stocks. However, as reported by Margolis (1963), it appears that *D. truttae* occurs in some sockeye from both east and west Kamchatka.

One of the limitations in the use of *T. crassus* and *D. truttae* as " natural tags " lies in the fact that they occur only in a minor proportion of the sockeye originating in Bristol Bay and Kamchatka, respectively. Hence, the origin of individual sockeye not infected with either parasite remains doubtful. Non-infected sockeye may have originated in either of these two areas or in some other area where neither parasite is found in sockeye. However, by using rates of *T. crassus* infection as a measure, it is possible to make some inferences regarding the relative proportions of Bristol Bay sockeye in high seas samples.

A brief account of the biology of *T. crassus* and *D. truttae* and a detailed discussion of their use in the determination of the oceanic distribution of Bristol Bay and Kamchatkan sockeye has been presented by Margolis (1963). The results presented below are based on his paper.

Oceanic Range of Bristol Bay and Kamchatkan Sockeye

Maturing sockeye. The distribution of maturing sockeye identified as having originated in Bristol Bay (i.e., infected with *T. crassus*) or Kamchatka (i.e., infected with *D. truttae*), in relation to the localities and numbers of fish sampled, are shown separately for the May-June and July-August periods of each of the years 1955 to 1959 in Figures 54 to 58. Figure 59 shows the overall distribution of Kamchatkan and Bristol Bay maturing sockeye for all years combined.

When all years are considered together, the results show that maturing Kamchatkan sockeye were found as far east as 175°E in the Bering Sea (up to mid-June) and as far east as 173°19′E in the North Pacific Ocean (from mid-May to early July). In a north-south direction they were distributed from almost 47°N to 58°N.

Maturing Bristol Bay sockeye occurred eastward to 145°W in the northern part (between 53°N and 58°N) of the Gulf of Alaska, and westward to 168°15′E in the North Pacific Ocean and to 171°E in the Bering Sea; they were found south to 50°N in the western North Pacific Ocean and north to 59°N in

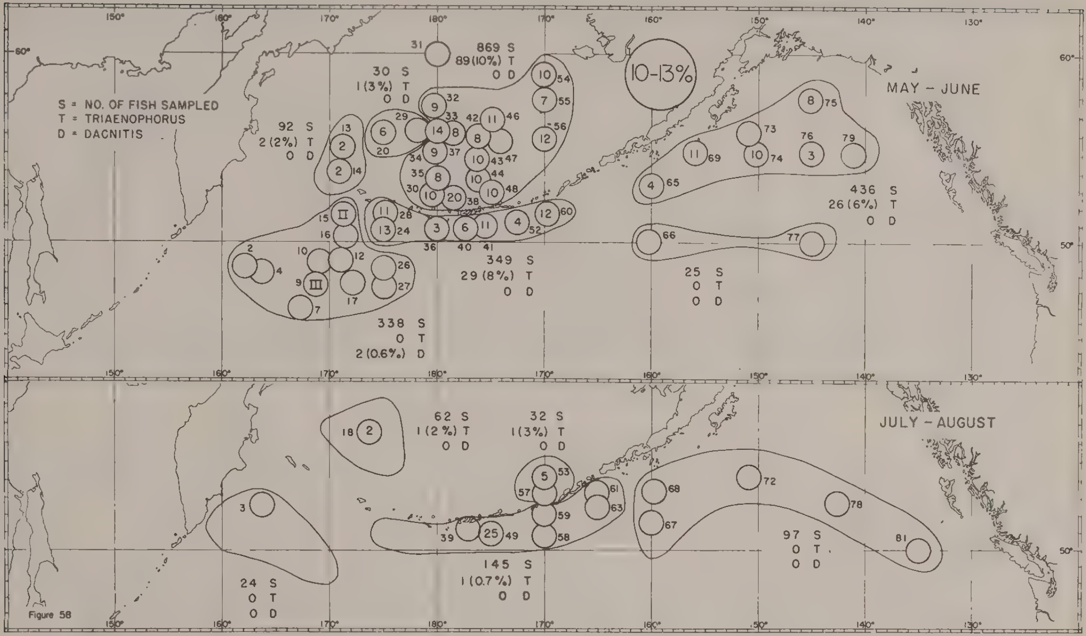

S = NO. OF FISH SAMPLED
T = TRIAENOPHORUS
D = DACNITIS
MAY – JUNE
10-13%
869 S 89 (10%) T 0 D
30 S 1 (3%) T 0 D
92 S 2 (2%) T 0 D
349 S 29 (8%) T 0 D
338 S 0 T 2 (0.6%) D
436 S 26 (6%) T 0 D
25 S 0 T 0 D
JULY – AUGUST
62 S 1 (2%) T 0 D
32 S 1 (3%) T 0 D
145 S 1 (0.7%) T 0 D
24 S 0 T 0 D
97 S 0 T 0 D
150°
160°
170°
180°
170°
160°
150°
140°
130°
60°
50°
Figure 58

FIGURE 58. Incidence of *Triaenophorus* and *Dacnitis* in high seas samples of maturing sockeye salmon in 1959. Samples of less than 9 sockeye are not shown individually, except at Station 49 (4 fish). Roman and Arabic numerals have the same significance as in Figure 56, except that station numbers are as given in Table XVI of Margolis (1963). (From Margolis, 1963, modified in the May–June chart to show the estimated overall rate of *Triaenophorus* infection in Bristol Bay adults, for comparison with high seas rates of infection.)

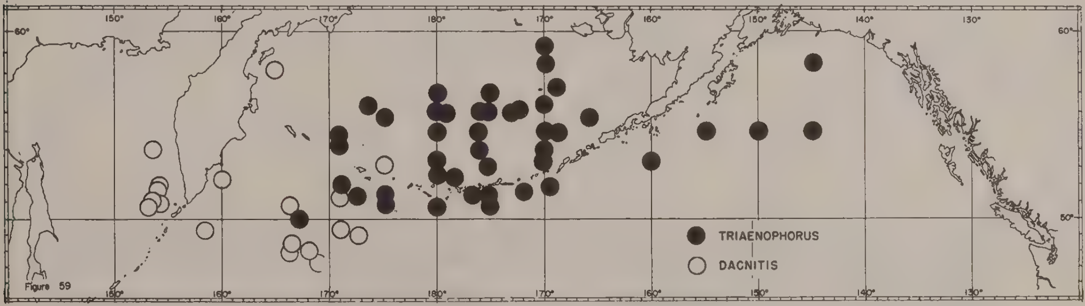

● TRIAENOPHORUS
○ DACNITIS
150°
160°
170°
180°
170°
160°
150°
140°
130°
60°
50°
Figure 59

FIGURE 59. Locations of high seas capture of *Triaenophorus*-infected and *Dacnitis*-infected maturing sockeye salmon from 1955 to 1959. Sampling locations at which neither parasite was found are not shown. (From Margolis, 1963.)

the eastern Bering Sea. This extensive distribution of Bristol Bay sockeye was observed almost entirely in the latter half of May and in June, with the later-caught fish generally having been taken closer to Bristol Bay. For example, in the eastern half of the Bering Sea they were taken almost entirely in the second half of June. However, a few maturing Bristol Bay sockeye also were found in the Bering Sea as far west as about 173°E in early July, and south of the mid-Aleutian Islands even as late as the beginning of August.

Because the majority of Kamchatkan and Bristol Bay sockeye do not carry a parasite which enables recognition of their area of origin, and because of certain limitations in sampling, with respect to area or time or numbers of fish, the distribution of matur-

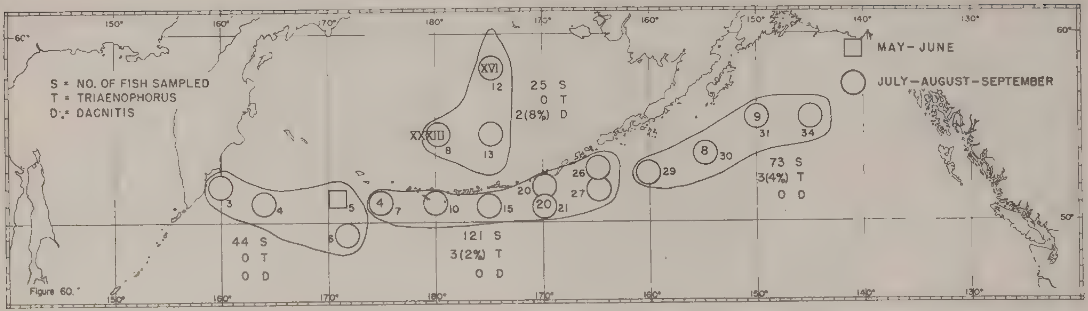

S = NO. OF FISH SAMPLED
T = TRIAENOPHORUS
D = DACNITIS
MAY-JUNE
JULY-AUGUST-SEPTEMBER
25 S
0 T
2(8%) D
73 S
3(4%) T
0 D
44 S
0 T
0 D
121 S
3(2%) T
0 D
Figure 60.

FIGURE 60. Incidence of *Triaenophorus* and *Dacnitis* in high seas samples of immature sockeye salmon in 1956. Samples of less than 8 sockeye are not shown individually, except at Station 8 (3 fish) and Station 12 (6 fish). Roman and Arabic numerals have the same significance as in Figure 56, except that station numbers are as given in Table XIII of Margolis (1963). (From Margolis, 1963.)

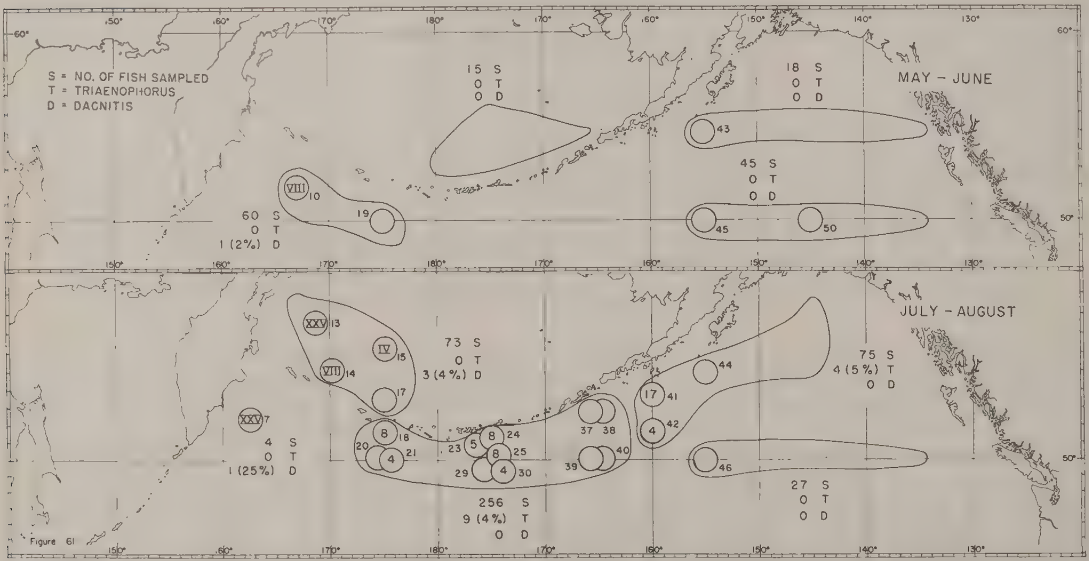

S = NO. OF FISH SAMPLED
T = TRIAENOPHORUS
D = DACNITIS
MAY - JUNE
15 S
0 T
0 D
18 S
0 T
0 D
45 S
0 T
0 D
60 S
0 T
1 (2%) D
JULY - AUGUST
73 S
0 T
3 (4%) D
75 S
4 (5%) T
0 D
4 S
0 T
1 (25%) D
256 S
9 (4%) T
0 D
27 S
0 T
0 D
Figure 61

FIGURE 61. Incidence of *Triaenophorus* and *Dacnitis* in high seas samples of immature sockeye salmon in 1957. Samples of less than 9 sockeye are not shown individually, except at Stations 7 and 13 (4 fish each). Roman and Arabic numerals have the same significance as in Figure 56. (From Margolis, 1963.)

ing Kamchatkan and Bristol Bay sockeye may extend over a wider oceanic zone than has been determined. Furthermore, since significant sampling in any of the years did not commence until about mid-May, the distribution of these sockeye stocks is entirely unknown prior to that time.

It is not possible, from the available data, to determine if real annual variations occurred in the distributional range of maturing Bristol Bay or Kamchatkan sockeye because of the many differences between years in area of coverage, level of sampling, and dates of sampling in specific regions. Also, since the likelihood of encountering a *Triaenophorus*-infected sockeye in a high seas sample of a given size (assuming it contained some Bristol Bay sockeye) is directly related to the incidence of infection in the Bristol Bay stocks, the apparent distribution of Bristol Bay sockeye may be affected by the annual variations in the estimated incidence of *T. crassus* in the Bristol Bay stocks. For example, a sample which might be adequate for detection of the presence of Bristol Bay sockeye in a year of high *T. crassus* rate of infection,

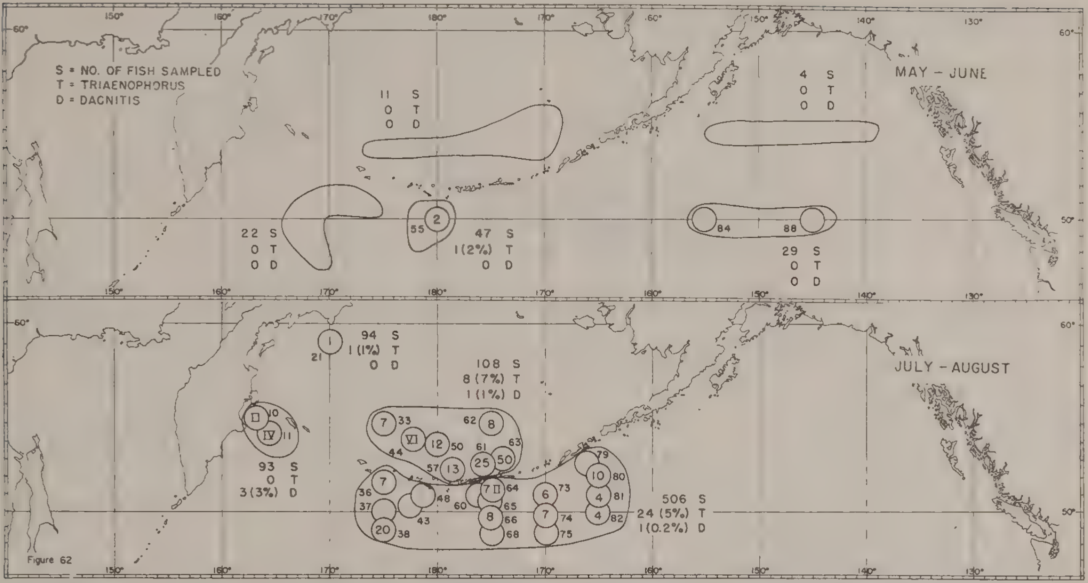

S = NO. OF FISH SAMPLED
T = TRIAENOPHORUS
D = DAGNITIS
MAY – JUNE
11 S 0 T 0 D
4 S 0 T 0 D
22 S 0 T 0 D
47 S 1(2%) T 0 D
29 S 0 T 0 D
JULY – AUGUST
94 S 1(1%) T 0 D
108 S 8(7%) T 1(1%) D
93 S 0 T 3(3%) D
506 S 24(5%) T 1(0.2%) D
Figure 62

FIGURE 62. Incidence of *Triaenophorus* and *Dacnitis* in high seas samples of immature sockeye salmon in 1958. Samples of less than 8 sockeye are not shown individually, except at Station 61 (4 fish) and Station 63 (2 fish). Roman and Arabic numerals have the same significance as in Figure 57. (From Margolis, 1963.)

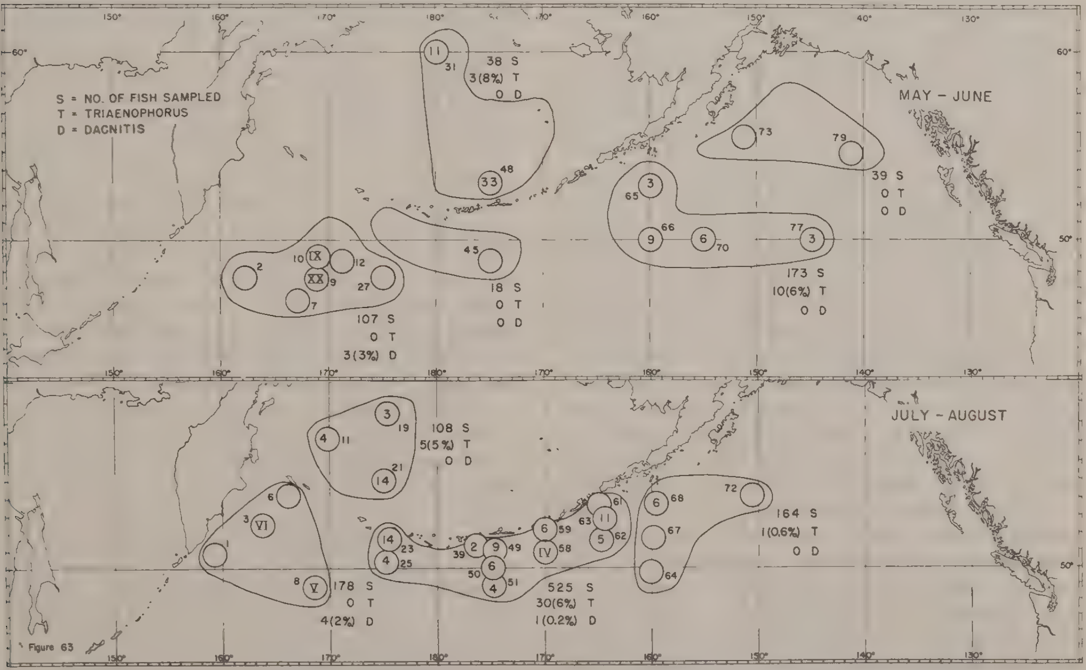

S = NO. OF FISH SAMPLED
T = TRIAENOPHORUS
D = DAGNITIS
MAY – JUNE
38 S 3(8%) T 0 D
39 S 0 T 0 D
18 S 0 T 0 D
107 S 0 T 3(3%) D
173 S 10(6%) T 0 D
JULY – AUGUST
108 S 5(5%) T 0 D
164 S 1(0.6%) T 0 D
178 S 0 T 4(2%) D
525 S 30(6%) T 1(0.2%) D
Figure 63

FIGURE 63. Incidence of *Triaenophorus* and *Dacnitis* in high seas samples of immature sockeye salmon in 1959. Samples of less than 9 sockeye are not shown individually, except at Station 48 (6 fish). Roman and Arabic numerals have the same significance as in Figure 58. (From Margolis, 1963.)

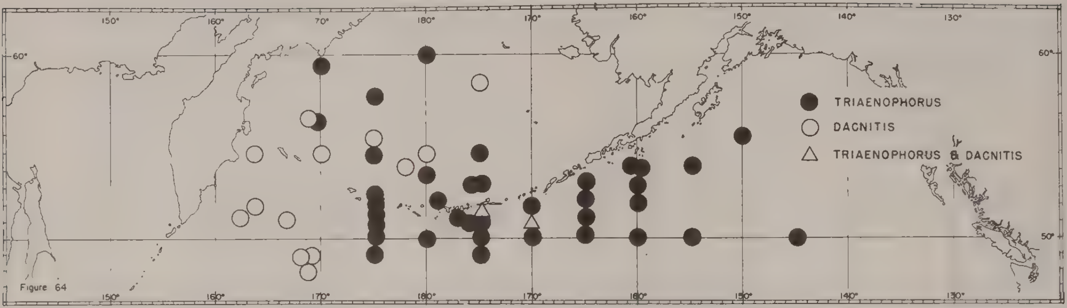


FIGURE 64. Locations of high seas capture of *Triaenophorus*-infected and *Dacnitis*-infected immature sockeye salmon from 1956 to 1959. Sampling locations at which neither parasite was found are not shown. (From Margolis, 1963.)

such as 1958 (22%), might not be at all adequate in a year of low *T. crassus* rate of infection, such as 1957 (3.2%). Hence, most of the observed differences between years in the distribution of maturing Bristol Bay or Kamchatkan sockeye may actually be nothing more than a reflection of variations in the aforementioned factors. The relatively few *Dacnitis*-infected sockeye obtained on the high seas, which presumably is the result of a low incidence of this parasite in Kamchatkan sockeye stocks, adds further to the difficulties in detecting if annual variations occur in the high seas distribution of Kamchatkan sockeye.

Immature sockeye. Figures 60 to 63 show the distribution of immature sockeye identified as having originated in Kamchatka or Bristol Bay, in relation to all samples examined, in the years 1956 to 1959. The distributions for each year are shown separately for the May-June and July-August periods. Figure 64 summarizes the locations of capture of Kamchatkan and Bristol Bay immatures in all years. From this figure it is seen that Kamchatkan immature sockeye occurred eastward to 170°W south of the Aleutians and to 175°W in the Bering Sea, and between latitudes 48°N in the North Pacific and 58°N in the Bering Sea. Bristol Bay immature sockeye were found from 145°W in the Gulf of Alaska (between 50°N and 56°N) westward to 175°E in the North Pacific (between the Aleutian Islands and 49°N), and in the Bering Sea between 175°W and 170°E as far north as 60°N. For the same reasons as discussed for maturing sockeye, the distribution of immature Bristol Bay and Kamchatkan sockeye may extend over even broader areas than has been observed. Most of the immature sockeye of both Bristol Bay and Kamchatkan origin were found in samples taken in July and August.

Only one Bristol Bay immature (from the south-central Gulf of Alaska in 1959) was identified in samples taken in May; several were obtained from late June samples, principally in the western Gulf of Alaska (in 1959) but also from the central Bering Sea (in 1959) and south of the mid-Aleutian area (in 1958).

A few immature Kamchatkan sockeye were taken in the northwest Pacific Ocean in late May (in 1959) and in late June (in 1957).

Annual variations in area of coverage, in time and level of sampling in specific areas, and in rates of infection with the parasite tags impose limitations on adequate between-year comparisons of the distribution of Bristol Bay and Kamchatkan immature sockeye. However, it seems likely that the overall range of distribution (i.e., when all years are considered together) of these stocks reflects, generally, the annual pattern of distribution. Considering Bristol Bay immatures, they occurred south of the Aleutians as far west as 175°E in each of the years 1956 to 1959; they were present in the central and western Bering Sea, west to about 170°E, in 1958 and 1959; and they were also observed in more than one year in the Gulf of Alaska. Although only 20 immature sockeye were identified as having originated in Kamchatka, individual records from south of the Aleutians in 1958 (at 175°W) and in 1959 (at about 170°W), and records from the Bering Sea in 1956 (at 180° and 175°W) and in 1958 (at 178°E) suggest that the occurrence of immature Kamchatkan sockeye as far west as the central Bering Sea and the central Aleutian area in July or August is probably a regular occurrence.

The distribution of one-ocean-winter[8] immature sockeye appears to be as extensive or almost as extensive as that of older immature fish of the same origin. Bristol Bay sockeye which had spent one year at sea were identified westward to 175°E both south of the

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[8] The terms " one-ocean-winter ", " two-ocean-winter ", etc., refer to sockeye which have completed one, two, etc., winters of residence at sea.

Aleutians and in the Bering Sea, and eastward to 155°W in the Gulf of Alaska, or almost as far east and west as older sockeye. Only two one-ocean-winter Kamchatkan sockeye were identified, but their locations of capture (175°W south of the Aleutians in early August and 178°E in the Bering Sea in mid-July) indicate a wide dispersal in the summer of Kamchatkan sockeye of this age group.

Oceanic Areas of Dominance of Bristol Bay Maturing Sockeye

By comparing rates of *Triaenophorus* infection in high seas samples of maturing sockeye with the overall rate of infection in the adults returning to Bristol Bay it is possible to arrive at some conclusions regarding the oceanic areas in which maturing Bristol Bay sockeye predominate. As discussed by Margolis (1963), this procedure assumes that maturing sockeye from individual Bristol Bay rivers are more or less homogeneously mixed during their last two months at sea.

The kinds of data on which the quantitative conclusions are based and the nature of these conclusions may be described briefly as follows. For maturing sockeye, groups of closely spaced samples in which the incidence of *T. crassus* infection is similar to the estimated overall incidence in Bristol Bay probably consist entirely or largely of sockeye of Bristol Bay origin; progressively decreasing rates of infection in a series of adjacent samples suggest decreasing proportions of Bristol Bay sockeye and consistent absence or rarity of *T. crassus* indicates absence or scarcity of Bristol Bay sockeye in the samples.

The incidence of *T. crassus* infection in individual high seas samples of maturing sockeye and in groups of samples are shown separately for the May-June and July-August periods of each of the years 1955 to 1959 in Figures 54 to 58. Also shown in the May-June charts of Figures 56 to 58 are the estimated overall rates of *T. crassus* infection in the adult runs returning to Bristol Bay in 1957 to 1959.

The discussion pertaining to the oceanic areas dominated by Bristol Bay maturing sockeye will be confined to the May-June period (except for the waters adjacent to the southwest coast of Kamchatka) because most of the sampling of maturing sockeye occurred during this period. In mid-ocean areas the abundance of maturing sockeye diminishes sharply in July and August. Also, only the years 1957 to 1959 will be considered because the data for the years 1955 and 1956 are too scanty. Four areas will be treated separately: (1) the Bering Sea, (2) the waters within 60 miles south of the Aleutians, west to 175°E, (3) the northwest Pacific from the southeast coast of Kamchatka to 175°E (exclusive of the immediate vicinity of the Aleutians at 175°E) and (4) the Gulf of Alaska.

Bering Sea. In the eastern Bering Sea, all, or at least the vast majority, of the maturing sockeye in samples taken in June were of Bristol Bay origin. Because of sampling limitations the western limit of this marked dominance of Bristol Bay sockeye could not be determined for any of the years of investigation, but it was at least 175°W in 1957, 170°W in 1958 and 180° in 1959.

Although it was not possible, in any year, to determine the western limit of the dominance of Bristol Bay maturing sockeye in the Bering Sea, fish of this origin formed a minor proportion of the samples taken at 171°E in June of 1959, indicating that in 1959 the western extent of the region of dominance of Bristol Bay sockeye in June occurred between 180° and 171°E. The results from the limited sampling of maturing sockeye from west of 178°W in the Bering Sea in late May and in June, 1958, suggest that it is unlikely that Bristol Bay sockeye dominated in this area. The individual samples were small so that it is not possible to state precisely the easternmost longitude at which Bristol Bay sockeye were not dominant. However, considering all samples together, the above conclusion seems warranted, and it appears that in 1958 the western extent in the Bering Sea of the area of dominance of Bristol Bay maturing sockeye lay between 170°W and about 180°.

South of the Aleutian Islands. Only data obtained from the 1959 samples provided information on the stocks of maturing sockeye dominating the area immediately south of the Aleutians westward to 175°E. Samples collected in late May and in early June from about 169°W to 175°E appeared to be predominantly of Bristol Bay origin, although the dominance was not as pronounced as in the eastern Bering Sea.

Northwest Pacific Ocean. From 175°E to the southeast coast of Kamchatka (excluding the waters immediately south of the Aleutians at 175°E), Bristol Bay sockeye were either absent or constituted a small proportion of the maturing sockeye in samples taken from mid-May to late July. Generally, the May-June samples were taken in the eastern part and the July samples in the western part of this region.

Gulf of Alaska. In the northern part of the Gulf of Alaska, in samples of maturing sockeye taken in late May and in the first half of June in 1958 and 1959, the proportions of Bristol Bay sockeye diminished towards the east. At 155°W a very large proportion of the sockeye were of Bristol Bay origin, whereas at 141°W (in 1959) Bristol Bay sockeye were absent or, at best, could not have formed a significant proportion of the fish in the sample. The eastern extent of the dominance of Bristol Bay sockeye appears to have been between 155°W and 150°W in 1958 and between 150°W and 145°W in 1959. This may indicate that there is annual variation in the area dominated by Bristol Bay sockeye, but, on the other hand, the differences between the two years may be a reflection of the somewhat later dates of sampling at 150°W and 145°W in 1958 than in 1959.

The rapid movement of Bristol Bay maturing sockeye out of the Gulf of Alaska appears to be indicated by two samples taken in 1959, about two weeks apart, at or approximately at 55°N, 150°W. A group of fish caught between May 25 and May 28 contained a very large proportion of Bristol Bay sockeye, whereas a sample taken on June 10 and June 11 contained few, if any, maturing Bristol Bay sockeye. However, as late as about mid-June Bristol Bay maturing sockeye were still well represented in the more western part of the northern Gulf of Alaska, as evidenced by their overwhelming dominance of the samples from 55°N, 155°W in 1958 and 1959.

EVIDENCE FROM MORPHOLOGY

Differences in the morphological characteristics of North American and Asian sockeye salmon were used by Fukuhara (1961), Fukuhara *et al.* (1962), Landrum and Dark (1963), and Dark and Landrum (1964) to determine the origin of sockeye salmon occurring in the North Pacific Ocean and Bering Sea.

In the studies of Fukuhara *et al.* (1962), certain morphological characters were selected to measure the racial differences between the sockeye from western Alaska and those from Kamchatka, and a discriminant function analysis was employed to classify sockeye caught in the Bering Sea and North Pacific Ocean. Samples of sockeye taken from the Okhotsk Sea off the coast of southwest Kamchatka and from the Bristol Bay-Chignik-Karluk river systems were chosen as representative of the sockeye originating in the two regions referred to above. These selections were based on evidence from tagging studies, parasite studies and generalized distance function analyses (INPFC, 1958 and 1959) which indicated that most of the maturing sockeye salmon in the Bering Sea and central and western North Pacific Ocean originated in Kamchatka or western Alaska. Information on the sizes of sockeye runs to various western Alaskan inshore areas showed that almost all western Alaskan sockeye originate in the rivers of Bristol Bay and in

TABLE 8. Errors of misclassification of sockeye salmon from the two reference areas in the years 1956 to 1961 in terms of the discriminant function based on 1956 data[1].

	1956	1957	1958	1959	1960	1961
For western Alaskan populations						
Bristol Bay						
Naknek R.	0.302	0.216	0.351	0.286	0.383	0.267
Egegik R.	0.157	0.189	0.157	0.143	0.291	0.201
Ugashik R.	0.176	0.233	0.134	0.141	0.207	0.215
Kvichak R.	0.150	0.152	0.189	0.226	0.166	0.134
Branch R.	—	—	—	—	0.576	0.569
Wood R.	0.352	0.408	0.254	0.236	0.282	0.228
Kodiak I.						
Karluk R.	0.276	0.225	0.293	0.325	—	—
Red R.	0.189	0.129	0.206	0.169	—	—
Chignik R.	0.213	0.126	0.139	0.180	—	—
Weighted average	0.178[2]		0.226	0.236	0.218	0.170
For Kamchatkan populations						
Ozernaia R.	—	—	—	0.366	—	—
Southwest offshore (Okhotsk Sea)	0.220	0.206	0.200	—	—	—
	0.204	0.256	0.328	—	—	—
	0.238	0.250	0.274	—	—	—
	0.261	—	0.361	—	—	—
Southeast offshore	—	—	—	—	0.225	0.374
	—	—	—	—	0.218	0.365
	—	—	—	—	0.349	—
Average	0.237		0.291	0.366	0.264	0.369

[1] From Fukuhara (1961), Fukuhara *et al.* (1962), Landrum and Dark (1963), and Dark and Landrum (1964).

[2] The weighted average error of misclassification for the 1956 and 1957 high seas samples was derived from the 1957 estimates by weighting them by relative abundance as estimated from combined escapements in 1956 and 1957.

the Chignik and Karluk rivers.[4] Because samples from Kamchatkan rivers were not available, the samples from the Sea of Okhotsk were used to determine the discriminant function.

Seven meristic characters were counted to measure the racial differences between sockeye from the two reference areas (lateral line scales, vertebrae, gill rakers, ventral gill rakers, pectoral fin rays, anal fin elements and position of the first haemal arch). Statistical tests showed that for each of these characters only rarely were there significant intra-area variations due to counting methods or to difference in sex, age, life history stage and time of sampling. Therefore, separate treatment of the data by sex, etc., for inter-area comparisons was considered not to be necessary in the subsequent analysis. The correlation between each character and fish length was determined to be small enough so that the effect of length selectivity of the gear by which samples were obtained was disregarded.

Using samples obtained at sea off southwest Kamchatka and from streams in western Alaska in 1956, the seven meristic characters were combined in a discriminant function. Two classificatory categories or morphotypes were defined in terms of the discriminant function and errors of misclassification of sockeye from the two reference areas were estimated (Table 8). Although a rule of classification was established by the discriminant function, the classificatory results were not free from bias in indicating the proportions of sockeye from the two reference areas. This type of bias was corrected by use of the estimated errors of misclassification. As noted by Fukuhara *et al.* (1962), in correcting bias, ideally in each high seas sample the error of misclassification should be weighted according to the relative abundance of the various constituent populations, because, as is shown in Table 8, the error of misclassification is different for the different reference populations. Since the composition of high seas samples is unknown, a weighted average error of misclassification was defined for western Alaskan sockeye as a whole. This was accomplished by weighting the error of misclassification for each run by its relative abundance as estimated from escapement counts.

Fukuhara *et al.* (1962) reported the classificatory results obtained by applying the discriminant function derived from the 1956 reference samples to high seas samples collected in 1956 and 1957. These authors also reported on the details of the statistical analyses, tests of underlying statistical assumptions, and empirical verification of the efficacy of the discriminant function. Classifications of the high seas samples taken in 1958 and 1959 and the development of confidence intervals for the classificatory results were discussed by Fukuhara (1961). For 1956 and 1957 (with errors of misclassification of approximately 21%), high seas samples of 150 to 200 fish

TABLE 9. Average percentages of maturing western Alaskan sockeye salmon in samples taken in May and June, 1956–61, in the Bering Sea and North Pacific Ocean, and which contained 80% or more maturing fish.[1][2]

	Mid-point of 5° interval						
	160°E	165°E	170°E	175°E	180°	175°W	170°W
Bering Sea							
1956	—	—	—	—	65 (1)	—	90 (1)
1957	—	—	—	—	74 (1)	90 (6)	87 (4)
1958	—	0 (1)	0 (1)	9 (1)	—	—	86 (4)
1959	—	—	39 (3)	—	78 (8)	84 (6)	70 (3)
1960	—	—	—	47 (2)	90 (2)	96 (8)	94 (5)
1961	—	—	—	—	72 (5)	66 (2)	85 (9)
Pacific Ocean							
1956	—	—	51 (2)	51 (5)	—	—	—
1957	23 (1)	14 (3)	28 (3)	—	—	—	—
1958	15 (1)	6 (2)	23 (3)	45 (2)	—	—	—
1959	14 (2)	5 (3)	12 (7)	26 (4)	85 (2)	73 (3)	76 (2)
1960	—	0 (2)	31 (4)	—	81 (3)	—	87 (3)
1961	—	2 (2)	15 (3)	66 (1)	—	68 (1)	—

[1] The numbers of samples used for computing the averages are shown in parentheses.

[2] Based on data in Fukuhara (1961), Fukuhara *et al.* (1962), Landrum and Dark (1963), and Dark and Landrum (1964), with deletion of samples containing less than 80% maturing fish; proportions of maturing fish in the samples were determined from examination of data on file at the U. S. Bureau of Commercial Fisheries Laboratory, Seattle.

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[4] Chignik and Karluk rivers are actually in the western part of the region known as central Alaska; for convenience they are grouped here with western Alaskan stocks.

had 90% confidence limits of about ±8%. For 1959 (with an error of misclassification of approximately 30%), the 90% confidence limits were about ±15%. Landrum and Dark (1963) used the discriminant function derived from the 1956 reference samples to classify the 1960 collections. The average error of misclassification for Bristol Bay salmon was weighted by the relative abundance of the component stocks in the 1960 escapement. Dark and Landrum (1964) classified samples taken from the high seas in 1961.

Maturing Sockeye

The classificatory results given by Fukuhara (1961), Fukuhara *et al.* (1962), and Landrum and Dark (1963) for samples collected from 1956 to 1960 did not deal separately with maturing and immature fish. The available samples were divided only by time periods into three groups—those taken in May and June, those taken in July and those taken in August. Dark and Landrum's (1964) results of classification of the 1961 samples pertained only to maturing sockeye caught mainly in May and June. In general, most samples taken in May and June consisted essentially of maturing fish.

From the results reported by Fukuhara (1961), Fukuhara *et al.* (1962), Landrum and Dark (1963), and Dark and Landrum (1964), the origins of maturing sockeye salmon taken on the high seas in May and June may be summarized as follows. In Table 9 the percentages of western Alaskan sockeye in late May and in June samples containing 80% or more maturing fish were averaged by 5° intervals of longitude for the North Pacific Ocean and for the Bering Sea, according to year of sampling. These averages are shown in Figure 65 and are referred to in 5° " bands " centered on the longitude indicated. These percentages show: (1) in the Bering Sea, in the 180° band and eastward, the average percentage of western Alaskan sockeye in the samples ranged from 65% to 96%. Westward from this band, the average percentage of western Alaskan sockeye in the samples decreased. In the 175°E band and westward, the average percentage of Kamchatkan sockeye ranged from 53% to 100%. (2) In the North Pacific Ocean, from the Asian coast to the 170°E band, the average percentage of Kamchatkan sockeye in the samples ranged from 49% to 100%. In the 175°E band, the average percentage of western Alaskan sockeye ranged from 26% to 66%. In the 180° band and eastward, the average percentage of western Alaskan sockeye ranged from 68% to 87%. (3) In the Bering Sea eastward from the 180° band and in the North Pacific westward from the 170°W band, sampling from 1956 to 1961 was sufficiently intensive to suggest that the approximate ranges of percentages cited above reflect the relative proportions of the southwest Kamchatkan and western Alaskan sockeye present in these areas at the time of sampling.

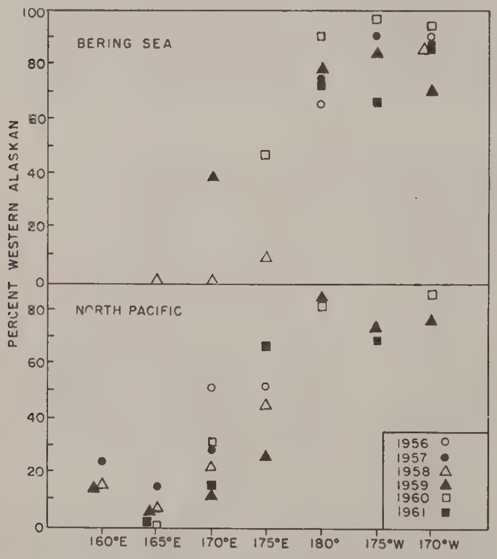

FIGURE 65. Average percentages of western Alaskan sockeye salmon in samples taken in May and June, 1956–61, in the Bering Sea and North Pacific Ocean, and which contained 80% or more maturing fish.

Immature Sockeye

As already noted, most of the samples taken in May and June consisted essentially of maturing fish; a very few were made up primarily of immatures. Data on file at the U.S. Bureau of Commercial Fisheries, Seattle, show that in July the proportion of immatures in the samples was variable and that in August the samples consisted almost entirely of immatures[5]. For a description of the general features of the distribution of immature western Alaskan and Kamchatkan sockeye the results of classification of the samples taken in July and August which contained 80% or more immature fish were used. The results of classifying the high seas samples have been averaged for 5° bands of longitude, as was done with the data for maturing sockeye. The results are shown in Table 10 and Figure 66.

In the Bering Sea there were only 10 samples available from 1956 to 1960. These samples showed

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[5] The proportion of maturing and immature sockeye in high-seas catches during various periods of the spring and summer were given by Manzer *et al.* (1965).

Table 10. Average percentages of western Alaskan sockeye salmon in samples taken in July and August, 1956-60, in the Bering Sea and North Pacific Ocean, and which contained 80% or more immature fish.[1][2]

	Mid-point of 5° interval								
	160°E	165°E	170°E	175°E	180°	175°W	170°W	165°W	160°W
Bering Sea									
1957	—	—	—	55 (5)	—	—	—	—	—
1958	—	—	—	0 (1)	40 (2)	—	—	—	—
1959	—	—	32 (2)	—	—	—	—	—	—
Pacific Ocean									
1956	—	—	—	82 (1)	70 (1)	42 (1)	—	—	—
1957	—	—	—	67 (4)	—	76 (8)	—	42 (1)	46 (2)
1958	—	12 (2)	—	29 (1)	24 (1)	40 (5)	52 (2)	47 (4)	—
1959	0 (1)	0 (2)	—	—	—	61 (3)	50 (1)	40 (2)	48 (4)
1960	—	—	6 (1)	54 (4)	74 (5)	71 (5)	63 (4)	—	—

[1] The numbers of samples used for computing the averages are shown in parentheses.

[2] Taken from Fukuhara (1961), Fukuhara *et al.* (1962), and Landrum and Dark (1963).

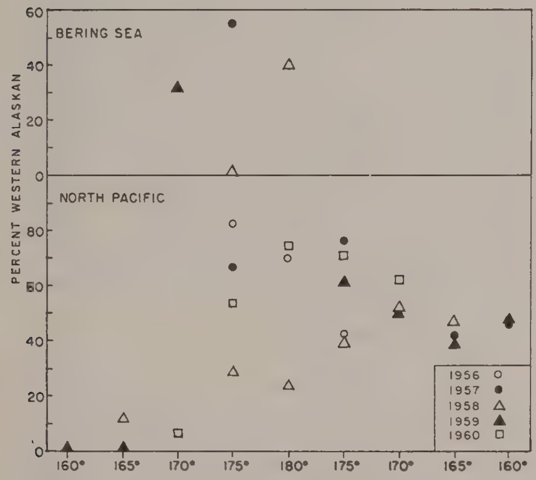

Figure 66. Average percentages of western Alaskan sockeye salmon in samples taken in July and August, 1956–60, in the Bering Sea and North Pacific Ocean, and which contained 80% or more immature fish.

that both Kamchatkan and western Alaskan sockeye were present in the 170°E, 175°E and 180° bands.

In the Pacific Ocean in the 170°E band and westward the samples appeared to contain few, if any, western Alaskan sockeye. From the 175°E band to the 175°W band the samples were generally classified as dominantly western Alaskan sockeye but there seemed to be annual variations. In 1958 the available samples classified predominantly as Kamchatkan.

The average proportions of immature western Alaskan sockeye appear to decrease in the 170°W and 165°W bands. As discussed later, North American sockeye originating south and east of Kodiak Island misclassified in large proportions as Kamchatkan sockeye by the discriminant function used in these morphological studies. Consequently, the apparent decrease in proportion of western Alaskan immature sockeye in the eastern Aleutian area may be due to the presence of increasing proportions of North American sockeye from south and east of Kodiak rather than to the presence of increasing proportions of Kamchatkan sockeye.

Discussion

In reviewing the morphological studies it appeared to us that three features should be more closely examined. The first concerns the samples employed as Kamchatkan standards in determining the error of misclassification for Kamchatkan sockeye. Because of a general lack of samples from Kamchatkan rivers (only one sample was available from the Ozernaia River in 1959), samples taken from the Okhotsk Sea were used from 1956 to 1958 as the Kamchatkan standard from which errors of misclassification were determined. After 1958, Okhotsk Sea samples were not available and in 1960 and 1961 samples taken off the southeast coast of Kamchatka were used as Kamchatkan standards. On the basis of age composition, the samples from off the southwest coast of Kamchatka (Okhotsk Sea) seem not to consist primarily of Ozernaia River sockeye, which is the main stock in west Kamchatka. The Ozernaia sockeye descend to the sea in their third year (Table 1 of Egorova *et al.*, 1961 ; Tables 11, 12, 13 of Hanamura, 1966), whereas the Okhotsk Sea samples contained a large proportion of fish which migrated to sea in their second year (data on file, U.S. Bureau of Commercial Fisheries, Seattle).[6] Furthermore, it is not likely that stocks from east Kamchatka are represented in the samples from the Okhotsk Sea. It appears that the Okhotsk Sea samples, in large measure, were drawn from the smaller west Kamchatkan stocks, such as the Bolshaia, Icha, and others.

In contrast to the samples from the Sea of Okhotsk, those from off southeast Kamchatka used as Kamchatkan standards probably included sockeye from the principal Kamchatkan stocks for the following reasons. Tagging studies showed that the maturing sockeye which are caught in the high seas mothership fishery west of 165°E were en route to streams of both east and west Kamchatka, including the Ozernaia and Kamchatka Rivers. The high seas salmon fishery off the southeast coast of Kamchatka must exploit the major Kamchatkan stocks, because the catch is too large to be supported to any great extent by the runs to the less productive rivers.

While it appears certain that the major Kamchatkan stocks were represented in the samples used as standards from off southeast Kamchatka, it is not possible to determine the relative proportions of the various stocks present in these samples.

Since the Okhotsk Sea samples were not mainly composed of fish from the major Kamchatkan stocks and since the precise composition by river of origin is unknown for the reference samples taken off southeast Kamchatka, a question arises regarding the suitability of the errors of misclassification determined from these samples as corrections applied to the classificatory results of the discriminant function.

In addition to the reference samples, samples have been drawn from the area off southeast Kamchatka each year from 1956 to 1961. The results of the classification of these samples suggest that the errors of misclassification determined from the offshore standard samples discussed above are generally acceptable for Kamchatkan sockeye as a whole. However, the considerable inter-sample variations in 1958 and in 1960 in the error of misclassification suggest that there are differences in the error of misclassification among Kamchatkan stocks, similar to the differences observed among western Alaskan stocks (Table 8).

A second problem concerns the fact that there are some North American stocks which misclassify largely as Kamchatkan sockeye by the discriminant function used. The stocks originating to the east and south of Kodiak Island fall into this category (Fukuhara *et al.*, 1962). The results of classification of the 1958 high seas samples (Fukuhara, 1961) indicate that large proportions of Kamchatkan sockeye occurred in the Gulf of Alaska between 145°W and 155°W. However, tagging studies have shown that the maturing sockeye occurring in this area arise almost entirely, if not entirely, in North America. Thus, in the Gulf of Alaska the apparent occurrence of large proportions of Kamchatkan fish is undoubtedly the result of misclassification of North American stocks from east and south of Kodiak. How far westward (south of the Aleutians) this type of misclassification affects the general classificatory results is not known.

Other North American stocks which largely misclassify as Kamchatkan are the small stocks of western Alaskan sockeye from north of Bristol Bay (which have not been included in the standard western Alaskan samples for determination of the error of misclassification) and at least some of the small stocks spawning in the Aleutian Islands, such as those from the Kuskokwim River (36%–46% misclassification in 1957), Salmon Lake (52% misclassification in 1957), Yukon River (52% misclassification in 1957) and Unalaska Island (99% misclassification in 1956). The effects of these large errors of misclassification would not be significant if fish from these areas were mixed at sea with the vastly larger runs from Bristol Bay. However, if they occur apart from Bristol Bay sockeye in some parts of the ocean, they would give classificatory results which would erroneously indicate high proportions of Kamchatkan fish.

Because there appears to be much the same variation among Kamchatkan stocks as is shown for western Alaskan stocks, it is possible that there are minor Kamchatkan stocks which show a high error of misclassification as western Alaskan sockeye. As in the case of western Alaskan sockeye, if these small stocks are well mixed with the larger Kamchatkan stocks, the effect would be small. Should they be found apart from the major runs, classification would provide erroneously high percentages of western Alaskan sockeye.

A third question to be considered concerns the application to all high seas samples of a weighted average error of misclassification for western Alaskan sockeye as a whole, as discussed on page 45, for correction of bias resulting from the classificatory procedures of the discriminant function.[7] Fukuhara *et al.* (1962) assumed uniform mixing of Bristol Bay sockeye at sea. There is no way to determine the extent to which this assumption is justified, and if it is not valid, the point estimates of the proportion of western Alaskan or Kamchatkan fish in high seas samples will be biased. It is evident from tagging experiments that sockeye from the Bristol Bay streams may be found mixed at sea. The tagging experiments cannot be tested for homogeneity of mixing because of unequal rates of recovery and reporting of tagged fish. Parasite studies (Margolis, 1963) have shown that in the samples taken east of 180° longitude in the Bering Sea the incidence of *Triaenophorus* generally was similar to the average for Bristol Bay. Although this can result from mixtures other than that in which the various Bristol Bay stocks are mixed at sea in much the same proportions as their relative abundance, the assumption of uniform mixing at sea appears to be a reasonable choice.

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[6] For a general reference to the age composition of sockeye in the Okhotsk Sea mothership catches, from which the morphological samples were taken, see Manzer *et al.* (1965). Age composition of samples from the Ozernaia River in 1956 and other Kamchatkan Rivers in 1956 and 1957, and of samples from the Sea of Okhotsk in 1956 and 1957, are given in Tables 3 and 5 of Mosher (1963)

[7] A similar question exists regarding mixing of Kamchatkan sockeye at sea. Although the average error of misclassification applied may be generally acceptable for Kamchatkan sockeye as a whole, the detailed information necessary to consider the problem more closely is not available.

As it is not possible to prove the assumption of homogeneous mixing, an alternative procedure may be followed without this assumption and under the condition that no definite information exists on the proportion of the different western Alaskan stocks in each high seas sample. With this procedure, which is described below, two extreme limits can be set, using available morphological data, for the expected proportions of sockeye originating from the two reference areas, i.e., western Alaska and Kamchatka. The estimate of each of these proportions will be indefinite between these two extremes, on each of which, from a statistical point of view, sampling variation or confidence limits should be superimposed. Any additional information, definite or suggestive, on the composition of western Alaskan sockeye for the sample in question could reduce the possible range between the two extremes set by morphological data alone.

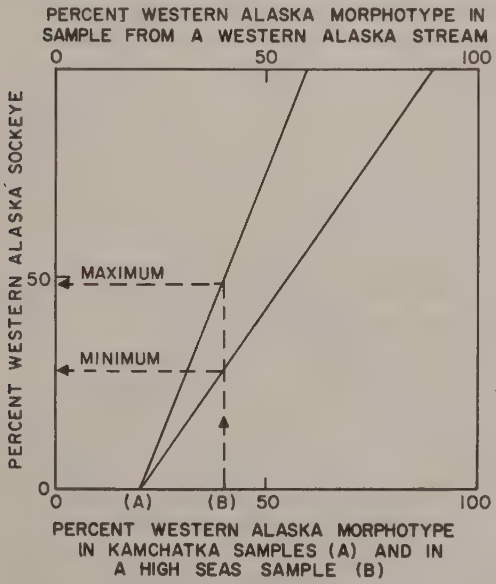


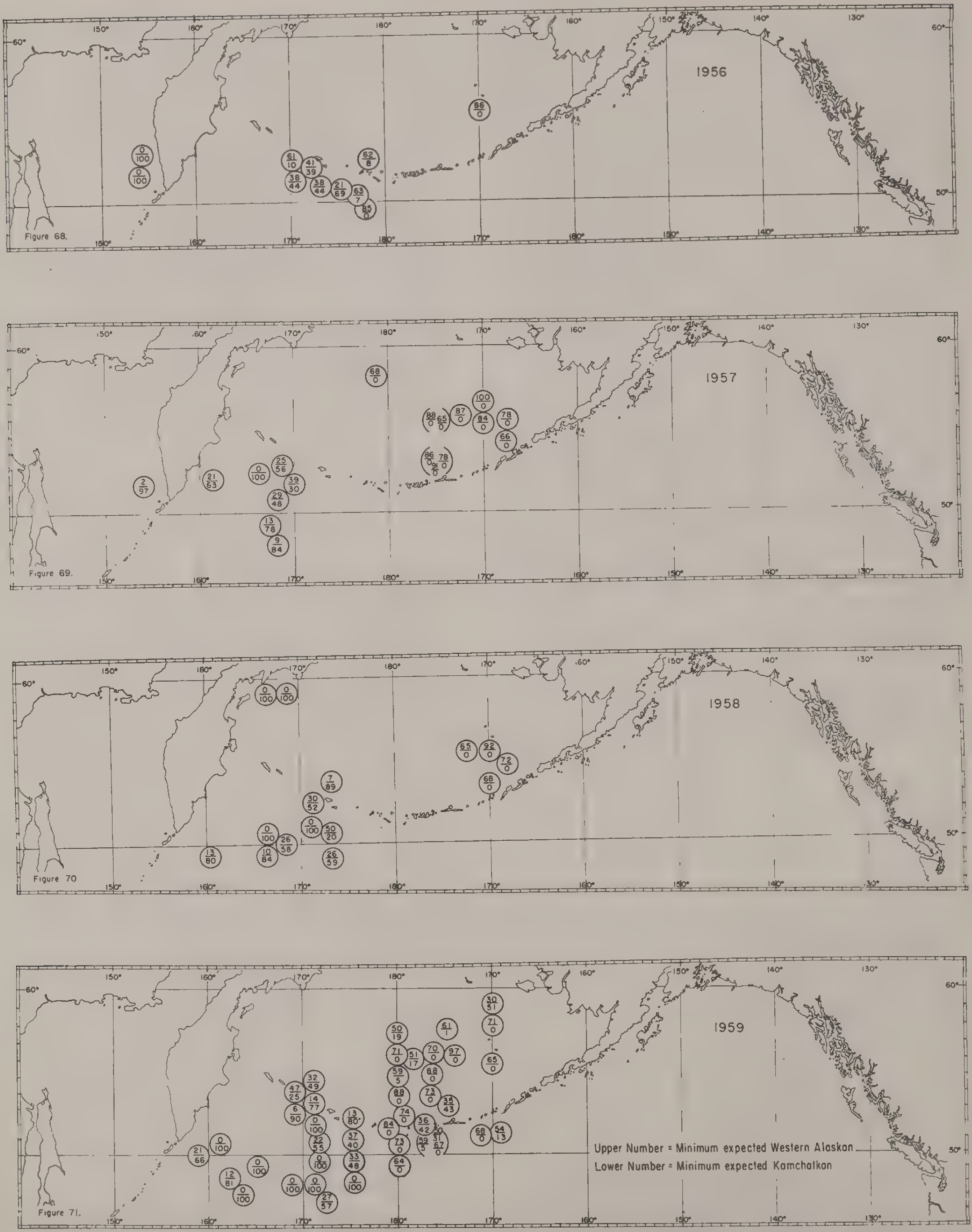
Figure 67. Estimation of minimum and maximum percentages of western Alaskan morphotype in samples taken at sea.

The procedures are explained by Figure 67. On the lower abscissa Kamchatkan sockeye (A) are represented in terms of the percentage misclassifying as western Alaskan sockeye and on the upper abscissa the proportions of the individual western Alaskan populations classifying as western Alaskan morphotype are represented. The diagonal lines are drawn from Kamchatkan sockeye on the lower abscissa to the two western Alaskan components which show the two extreme percentages of western Alaskan morphotype on the upper abscissa.

Western Alaskan sockeye defined in the morphological studies under consideration, that is, weighted by relative abundance of each component run, would lie between the two extreme western Alaskan components. Now, given the proportion of western Alaskan morphotype in a high seas sample, plotted on the lower abscissa (B), then the two extremes (minimum and maximum) for the expected proportion of western Alaskan sockeye will be obtained on the ordinate, as shown in Figure 67. Confidence limits could be calculated separately for these two extremes by the formula suggested by Fukuhara (1961).

In 1960 and 1961, Branch (Alagnak) River sockeye were included for the first time with the western Alaskan sockeye stocks from which the weighted average error of misclassification of these stocks as a whole was determined (Table 8). The error of misclassification of Branch River sockeye was considerably higher (57.6% in 1960 and 56.9% in 1961) than that of the other stocks included in the western Alaskan standard (the closest error was that for the Wood River in 1957—40.8%). Consequently, the inclusion of Branch River sockeye in the above-described procedure to determine the minimum proportion of Kamchatkan sockeye in high seas samples would result, in general, in lower minimum proportions than when the Branch River stocks are not included, assuming that the high error of misclassification of Branch River sockeye is an annual occurrence.

The results, based on the above procedure, for the samples taken in May and June which were composed of 80% or more maturing fish are shown in Figures 68 to 73. In these figures are shown the minimum expected proportion of maturing western Alaskan sockeye and the minimum expected proportion of


1956
Figure 68.
1957
Figure 69.
1958
Figure 70
1959
Figure 71.
Upper Number = Minimum expected Western Alaskan
Lower Number = Minimum expected Kamchatkan
150°
160°
170°
180°
170°
160°
150°
140°
130°
60°
50°

FIGURES 68–71. Estimated minimum percentages of maturing Kamchatkan and western Alaskan sockeye salmon in morphological samples, 1956–59 (May–June).

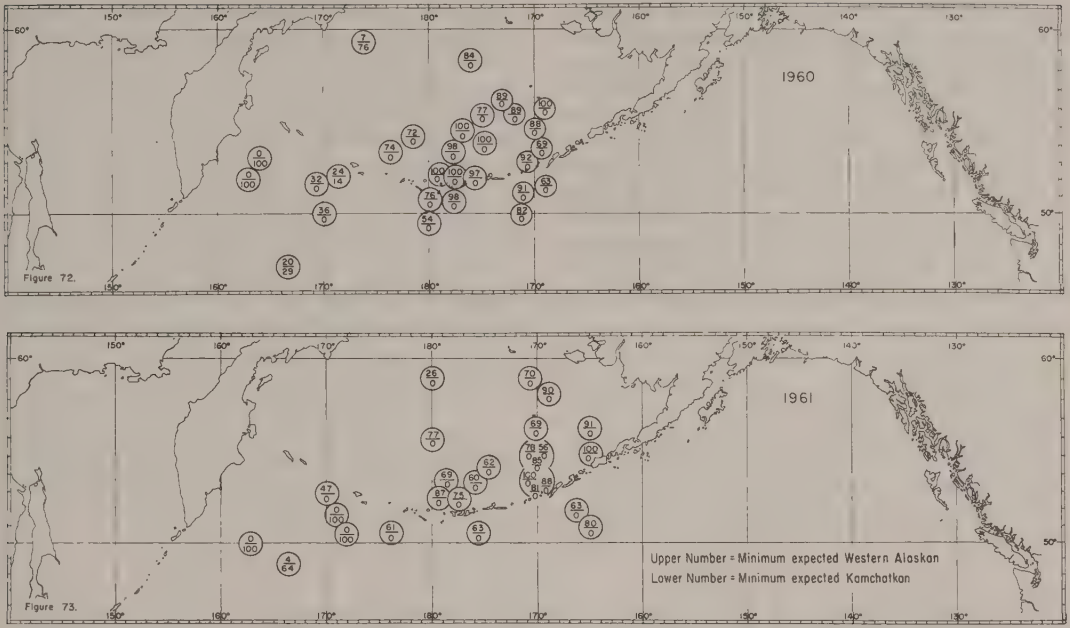


Figure 72.
1960
7/76
84/0
89/0
77/0
89/0
100/0
100/0
88/0
72/0
100/0
69/0
74/0
98/0
92/0
0/100
0/100
24/14
32/0
100/0
100/0
97/0
91/0
63/0
76/0
98/0
36/0
54/0
82/0
20/29
Figure 73.
1961
26/0
70/0
90/0
77/0
69/0
91/0
78/0
56/0
85/0
100/0
62/0
69/0
60/0
100/0
88/0
81/0
47/0
87/0
75/0
0/100
63/0
80/0
0/100
61/0
63/0
0/100
4/64
Upper Number = Minimum expected Western Alaskan
Lower Number = Minimum expected Kamchatkan
150°
160°
170°
180°
170°
160°
150°
140°
130°
60°
50°

Figures 72–73. Estimated minimum percentages of maturing Kamchatkan and western Alaskan sockeye salmon in morphological samples, 1960–61 (May–June).

maturing Kamchatkan sockeye (the complement of the maximum proportion of western Alaskan sockeye) in each sample for each of the six years, 1956 to 1961.

Although sampling coverage was not consistent over the whole area under consideration, some general conclusions can be drawn from the results presented in Figures 68 to 73. These conclusions are identical with those which would be arrived at from a study of the point estimates (and 90% confidence limits) of the proportion of maturing western Alaskan sockeye in high seas samples as presented by Fukuhara (1961), Fukuhara *et al.* (1962), Landrum and Dark (1963), and Dark and Landrum (1964), which were summarized earlier, and may be stated as follows:

(1) Western Alaskan and Kamchatkan sockeye seem to intermingle with each other over a wide range of the North Pacific and the Bering Sea. Western Alaskan sockeye were distributed to about 170°E and possibly farther westward in the North Pacific. It is not clearly defined under the present framework in the morphological study if maturing Kamchatkan sockeye were distributed eastward beyond 180°.

(2) Western Alaskan sockeye dominated as far west as 180° in the Bering Sea, and probably to the same longitude in the North Pacific. Kamchatkan sockeye dominated as far east as about 170°E in the North Pacific and probably as far east as about 175°E in the Bering Sea, at least in the northern part along the Kamchatkan coast.

(3) Between 170°E and 180° south of the Aleutians neither group of sockeye consistently dominated over the other.

Evidence from Scale Studies

Gilbert (1914–1916; 1918–1920) noted and described differences in scale patterns between races of Fraser River salmon on their spawning grounds. Various scientists since that time have used sockeye salmon scales in assigning fish of unknown origin to a particular spawning group. Scales of fish from different streams often have unique patterns. The use of scales for identification of the origin of sockeye salmon in the high seas is particularly attractive. When compared to other means of identifying high seas fish, scales are found to be relatively inexpensive to collect, store and examine. Consequently, there has been a considerable amount of study designed to develop means of determining the origin of high seas sockeye salmon using scales.

Studies by the U.S.S.R.

Krogius (1958) discussed the variation in Kamchatkan sockeye salmon scales in considerable detail. She described the patterns found in the Kamchatka, Bolshaia, Ozernaia, Kukhtui, Pylga and Paratunka rivers, which include the major sources of sockeye salmon in Asia. Distinctive differences were found in the number of circuli formed in each year of freshwater life, the size of the scale at the end of each year and the relative numbers of crooked or broken circuli. Using these features, she identified sockeye salmon from the Kamchatka, Ozernaia and Bolshaia rivers in samples taken in the North Pacific Ocean from Kamchatka to about 175°E. She stated that the origins of fish taken in the ocean could be determined from scales, but that the method is in need of further development.

Studies by Japan

Kubo (1958) reported the results of studies of sockeye salmon scales and developed a method which he employed to identify the origin of maturing 5_2 and 6_3 salmon caught on the high seas. His scale comparisons included: (1) total radius (anterior), (2) length of anterior field for ocean growth only, (3) the ratio of (2)/(1), (4) the ratio of the spacing of ocean circuli 21 to 30 to ocean circuli 11 to 20, and (5) the anterior radius of the freshwater zone excluding the so-called " plus growth ". Plus growth is the zone of widely spaced circuli which in some fish follows the last freshwater annulus and is believed to occur in fresh water just prior to migration to the sea. He determined that the radius of the freshwater growth zone was most efficient in identifying the origin of sockeye salmon in the high seas. He constructed frequency curves of freshwater radii and employed these to correct for overlap in this character between Kamchatkan and western Alaskan sockeye salmon.

The method employed by Kubo promises to be useful in determining the origin of salmon. His test for scale differences between sexes and the effect of fish length on scale characters might be improved by

TABLE 11. Age composition of Bristol Bay sockeye salmon runs (in millions of fish)[1].

Year	District	4_2	5_3	Sub-total 2-ocean	5_2	6_3	Sub-total 3-ocean	Total
1956	Nushagak	0.914	0.316	1.230	1.090	0.126	1.216	2.446
	Naknek-Kvichak	10.371	6.701	17.072	1.045	1.003	2.048	19.120
	Ugashik	0.528	0.129	0.657	0.049	0.057	0.106	0.763
	Egegik	0.292	1.326	1.618	0.201	0.418	0.619	2.237
	Total	12.105	8.472	20.577	2.385	1.604	3.989	24.566
	Percent	49.3	34.5	83.8	9.7	6.5	16.2	
1957	Nushagak	0.267	0.033	0.300	0.659	0.069	0.728	1.028
	Naknek-Kvichak	0.018	1.953	1.971	5.187	1.217	6.404	8.375
	Ugashik	0.130	0.117	0.247	0.261	0.062	0.323	0.570
	Egegik	0.015	0.158	0.173	0.260	0.738	0.998	1.171
	Total	0.430	2.261	2.691	6.367	2.086	8.453	11.144
	Percent	3.9	20.3	24.2	57.1	18.7	75.8	
1958	Nushagak	1.139	0.137	1.276	0.946	0.084	1.030	2.306
	Naknek-Kvichak	0.181	0.561	0.742	0.080	0.908	0.988	1.730
	Ugashik[2]	0.024	0.381	0.405	0.234	0.085	0.319	0.724
	Egegik	0.002	0.406	0.408	0.050	0.257	0.307	0.715
	Total	1.346	1.485	2.831	1.310	1.334	2.644	5.475
	Percent	24.6	27.1	51.7	23.9	24.4	48.3	
1959	Nushagak	2.888	1.320	4.208	0.436	0.097	0.533	4.741
	Naknek-Kvichak[2]	1.307	2.684	3.991	1.030	0.342	1.372	5.363
	Ugashik[3]							
	Egegik[3]							
	Total	4.195	4.004	8.199	1.466	0.439	1.905	10.104[4]
	Percent	41.5	39.6	81.1	14.5	4.3	18.9	

[1] From research files of the University of Washington Fisheries Research Institute and the U. S. Bureau of Commercial Fisheries, Seattle.

[2] Age composition estimated from catch samples only.

[3] Not available.

[4] Total run to the four districts was 12.622 million fish in 1959. Thus, the percentages given fairly accurately depict age composition of total Bristol Bay run in 1959.

utilizing fish of a single, known origin instead of a high seas sample of unknown, and perhaps mixed, origin. A mixture of fish with varying scale characters might obscure the relationships he was examining. However, it is doubtful that any large error has been introduced. The most serious difficulty arises from the use of only the 5_2 and 6_3 fish. The failure to include the 4_2 and 5_3 groups makes it impossible to interpret the results in terms of the relative proportions of Kamchatkan and Bristol Bay sockeye which may be present in the area. The proportion of the runs which return as 4_2, 5_3, 5_2, or 6_3 fish to Kamchatka or Bristol Bay varies widely from year to year. If only part of the fish are considered for any one year, it is easily possible to omit from consideration the major part of the maturing fish present.

This is illustrated by the estimated numbers of fish of ages 4_2, 5_3, 5_2 and 6_3 which returned to Bristol Bay streams from 1956 to 1959 (Table 11). These numbers are based on combined catch and escapement. In 1956, 20.5 million of the 24.5 million fish returning to Bristol Bay were 4_2's and 5_3's. Only 16% of the run was composed of 5_2 and 6_3 fish. The situation was reversed in 1957; about 8.5 million returned as 5_2 and 6_3 fish and they formed about 76% of the run of 11.1 million sockeye salmon. Therefore, in a study in which only 5_2 and 6_3 fish were used, if the ocean distribution was the same for all age categories, estimates of the percentage of the fish present of Bristol Bay origin would be expected to be very low in 1956 and high in 1957. In the Ozernaia River (west Kamchatka) there are no 5_2 sockeye and in 1956 and 1957, 6_3 fish formed 36% and 54%, respectively, of the runs returning to this river (Table 1 of Egorova *et al.*, 1961); in the Kamchatka River (east Kamchatka) the 5_2 and 6_3 fish formed 82% of the run returning in 1957 (Table 9 of Hanamura, 1966).

Taking into account the data in Table 11, it appears that the estimates of the numbers of Asian fish given by Kubo (1958) for the North Pacific Ocean are probably high, because only 1956 samples are considered. Bristol Bay fish would be under-represented. The run to Bristol Bay was relatively large in that year, but the dominant age categories involved did not enter the calculations. The degree to which bias occurs is determined by the relative proportions of fish of the same age categories in the runs to Kamchatka and Bristol Bay, and by whether fish from both origins are present at the time and place of sampling.

Kubo and Kosaka (1959) reported also a similar study which was concerned only with the origin of 5_3 sockeye salmon caught on the high seas. Because the anterior radius of the freshwater zone (from the focus to the last freshwater annulus) was distinctly larger in Naknek River (Bristol Bay) fish which matured as 5_3's than in those which remained in the ocean and matured as 6_3's they concluded that the radius of the freshwater zone was not suitable for use in separating Kamchatkan and Bristol Bay sockeye salmon. The maturity of high seas samples was not considered to be known with sufficient certainty and, therefore, a 5_3 fish taken at sea might actually have remained to migrate as a 6_3 fish a year later.

They found that the anterior radius of the freshwater zone divided by the combined width of the first two ocean zones provided the best means of identifying the origin of sockeye salmon in the Aleutian Islands area. Although it was not explicitly stated, the 1956 samples from the Kamchatka region and from Bristol Bay were evidently employed to define the population parameters which were used to calculate the percentage of high seas fish of Kamchatkan and Bristol Bay origin. Kubo and Kosaka's 1959 results are also difficult to interpret for the same reasons as discussed in connection with Kubo's 1958 report.

Studies by the United States

A study similar to that of Kubo (1958) and Kubo and Kosaka (1959) is reported by Mosher (1963). He used sockeye salmon scale samples taken in or near Kamchatka and in Bristol Bay streams (with some exceptions which are noted later) for continental standards and to test the efficiency of classificatory procedures. Each continental standard consisted of three components: sockeye which had migrated to sea in their second, third or fourth year of life. For the first two groups he used the numbers of circuli in fresh water and in the first year in the ocean as racial characters. For fish which migrated in their fourth year, he used the anterior radius of the freshwater zone and the length of the first year in the ocean zone. Because fish that had migrated to sea in their fourth year were uncommon in the Bristol Bay samples, he incorporated fish of these ages from the Karluk, Chignik and Kuskokwim rivers as well as other localities. This could bias classification of fish which had migrated to sea in their fourth year. Statistical comparisons of the means and variances of the characters selected indicated that the data for the two sexes could be combined for this study.

The fish were divided according to whether they had migrated to sea in their second, third or fourth years and whether the sample came from Kamchatka or Bristol Bay streams. For each of the six categories a bivariate tabulation was made of the number of circuli in the freshwater and first ocean year zones, except for fourth-year fish, when length of these zones was used. The bivariate frequencies were then weighted to 100 to adjust for unequal sample size. Next, the frequencies were superimposed, the Kamchatkan frequencies being placed on those for Bristol Bay of the same freshwater age. The numbers in each cell were compared and each cell was judged to be Kamchatkan or Bristol Bay according to which had the larger frequency.

When the 1957 samples of maturing fish of known origin which were used to construct the tables were identified by using the bivariate charts, 85.4% of the fish from near Kamchatka and 86.5% of the fish from Bristol Bay were correctly identified. Of an additional 261 scale samples from near or in Kamchatka in 1957 which were not used in deriving the continental standards (for lack of data on the area of the fish from which scales were taken), 237 (91%) were correctly assigned to Kamchatka.

Samples of fish taken in other years were also used to examine the accuracy of the classificatory procedure. Of 648 sockeye salmon taken in or near Kamchatka and 786 sockeye taken from Bristol Bay in 1956, 77.2% and 82.3%, respectively, were correctly identified.

For 1955 samples (again using the 1957 reference data), 77% of 168 Asian fish and 72% of 303 Bristol Bay fish were correctly identified. The average misclassification was roughly 14% for the 1957 samples, 21% for the 1956 samples and 25% for the 1955 samples. This seems to indicate a moderately increasing error in classification as the year in which the standards were taken becomes more remote.

Using the bivariate charts developed with 1957 inshore samples, Mosher (1963) classified the sockeye salmon in high seas samples collected in 1956 and 1957. The classificatory results were adjusted in 1956 and 1957 by a mean error of misclassification. This was derived by (1) averaging separately the errors for the individual Kamchatkan samples and those for the western Alaskan samples and (2) rounding the mean of the Kamchatkan and western Alaskan averages.

Mosher *et al.* (1961) applied the same method to the 1958 high seas samples. Using 1958 samples taken near Kamchatka, an average error of misclassification of 28.8% was determined for 584 Kamchatkan fish; using Bristol Bay samples a 15.6% error was determined for Bristol Bay fish. These errors were applied as adjustment factors to estimate the proportions of Kamchatkan and Bristol Bay (western Alaskan) sockeye in the high seas samples.

The high seas samples used by Mosher (1963) and by Mosher *et al.* (1961) were collected during the period of about mid-May to mid-July. In a number of cases these authors presented classificatory results of combined samples which covered broad time intervals or came from widely spaced locations, or both. Also, no information was given on the state of maturity of the fish in the various samples. For these reasons it was necessary to check the original data in order to describe the general features of the high seas distribution of maturing Bristol Bay and Kamchatkan sockeye in the months of May and June as determined by scale characters. These data were made available to us by the U.S. Bureau of Commercial Fisheries at Seattle. The period May-June was selected because, as noted in the morphology section, most of the samples obtained during this period consisted essentially of maturing fish and in July immature fish comprised large proportions of mid-ocean samples.

The samples we used in determining the area of origin of maturing sockeye taken on the high seas in May and June are listed in Table 12 for each of the years 1956, 1957 and 1958. Samples are shown separately by location, but samples taken within a one-week period at the same location were combined. Only maturing fish are included in the samples and only samples (or combined samples where this applies) which consisted of 20 or more fish were used. For each of these samples Table 12 shows the number of sockeye classified as Kamchatkan and western Alaskan by Mosher and co-workers. The proportions which classified as western Alaskan were adjusted by us for 1956 and 1957 samples following Mosher's (1963) procedure, and for 1958 samples following Mosher *et al.* (1961).

In Table 12 the results of these classifications are shown for each of the three years.

Results of classification of samples. In 1956 only two samples (at 178°E and 170°W) were available in the Bering Sea during May and June. Both were predominantly western Alaskan sockeye. In the North Pacific Ocean seven samples were available from 171°E to 176°E. Western Alaskan sockeye were predominant in four samples and Kamchatkan sockeye were predominant in three.

The 1957 sampling was broader than that in 1956. Samples from the Bering Sea (10) from 175°E to 166°W were predominantly western Alaskan sockeye. Kamchatkan sockeye dominated all seven samples from the North Pacific Ocean (166°E to 175°E).

Fewer samples were available in 1958. In the Bering Sea, Kamchatkan sockeye dominated the single sample at 166°E and western Alaskan sockeye dominated in the four samples near 170°W. Seven samples are shown between 167°E and 173°E in the North Pacific Ocean. Kamchatkan sockeye were strongly dominant in five of these and western Alaskan sockeye were weakly dominant in two.

TABLE 12. Classification of maturing sockeye salmon in high seas samples in May and June of 1956, 1957 and 1958, by means of scale characteristics.

Sampling location	Date	No. of fish	No. western Alaskan	No. Kamchatkan	Percent western Alaskan	Adjusted percent western Alaskan
52°N, 171°E	6/5, 1956	79	45	34	57.0	62.0
52°N, 171°E	6/15 »	132	59	73	44.7	41.0
52°N, 172°E	6/15 »	78	34	44	43.6	39.3
52°N, 174°E	6/5 »	69	41	28	59.4	66.2
50°N, 175°E	6/16 »	28	12	16	42.9	38.0
51°N, 176°E	5/25 »	35	23	12	65.7	77.0
50°N, 176°E	5/28 »	71	45	26	63.4	73.0
53°N, 178°E	6/26 »	148	94	54	63.5	73.2
56°N, 170°W	6/20 »	114	85	29	74.6	92.4
53°N, 166°E	6/20, 1957	63	4	59	6.3	0.0
49°N, 167°E	5/31 »	43	7	36	16.3	3.3
53°N, 168°E	5/25 »	39	16	23	41.0	37.7
48°N, 168°E	5/21 »	39	3	36	7.7	0.0
51°N, 169°E	5/21 »	33	16	17	48.5	48.0
51°N, 170°E	5/27 »	36	11	25	30.6	23.2
53°N, 175°E	6/14 »	1	1	0	75.0	84.5
53°N, 175°E	6/20 »	19	14	5		
50°N, 175°E	6/6 »	10	7	3	66.7	73.5
50°N, 175°E	6/10 »	23	16	7		
50°N, 175°E	6/11 »	9	4	5		
50°N, 175°E	6/12 »	9	7	2		
58°N, 179°E	6/27 »	49	34	15	69.4	76.8
53°N, 180°	6/22 »	33	24	9	72.7	81.5
56°N, 175°W	6/29 »	4	3	1	91.2	100.0
56°N, 175°W	6/30 »	32	30	2		
56°N, 175°W	6/15 »	169	146	23	86.4	100.0
53°N, 175°W	6/8 »	42	37	5	87.9	100.0
53°N, 175°W	6/9 »	47	42	5		
53°N, 175°W	6/10 »	35	30	5		
56°N, 173°W	6/17 »	131	99	32	75.6	85.5
57°N, 170°W	6/18 »	81	63	18	79.1	90.5
57°N, 170°W	6/19 »	58	47	11		
56°N, 168°W	6/21 »	56	49	7	87.5	100.0
56°N, 166°W	6/22 »	75	56	19	70.9	79.0
56°N, 166°W	6/23 »	17	9	8		
56°N, 166°W	6/24 »	11	8	3		
58°N, 166°E	6/22, 1958	8	4	4	45.0	39.3
58°N, 166°E	6/25 »	8	4	4		
58°N, 166°E	6/26 »	4	1	3		
51°N, 167°E	6/15 »	77	18	59	23.4	0.0
50°N, 168°E	5/16 »	88	36	52	40.9	22.0
48°N, 170°E	5/26 »	85	25	60	29.4	1.0
52°N, 172°E	6/5 »	75	43	32	57.3	51.5
51°N, 172°E	5/29 »	80	31	49	38.8	18.4
51°N, 172°E	6/7 »	92	54	38	58.7	54.0
49°N, 173°E	5/16 »	67	31	36	46.3	31.7
56°N, 172°W	6/18 »	62	53	9	85.5	100.0
56°N, 170°W	6/26 »	25	20	5	80.0	92.2
53°N, 170°W	6/17 »	48	39	9	81.2	94.5
55°N, 169°W	6/25 »	49	37	12	75.5	84.0

Discussion. Examination of the procedures employed by Mosher (1963) and Mosher *et al.* (1961) in assigning individual fish to western Alaska or Kamchatka and in applying corrections for errors of misclassification has directed attention to unanswered questions regarding the procedures. These are related mainly to an implied postulate, to the precision of the errors of misclassification used and to the adequacy as standards of the inshore samples available.

In using the bivariate tables and the accompanying errors of misclassification, it is implied that Kamchatkan sockeye from different streams are found everywhere at sea in the same proportions and with the same age composition as occurred in the combined inshore samples for Kamchatka, and likewise that western Alaskan sockeye from different streams are found at sea in the same proportions and in the same age composition[8] as they were represented in the inshore samples. The effect of any departure from this postulate cannot be measured from available data.

As previously described, the errors of misclassification which were used to adjust the 1956 and 1957 data are the means of the unweighted average errors for Kamchatkan and western Alaskan samples. This appears to bias the results. In 1956 a rounded average error of misclassification of 21% was calculated from 23.6% misclassification for Kamchatkan and 17.7% misclassification for western Alaskan sockeye. This over-adjusts the western Alaskan portion by 3.3% and under-adjusts the Kamchatkan portion by 2.6%, thus biasing the results to increase the apparent number of western Alaskan fish in the high seas samples. In 1957 a rounded average of 14% was used. This produced a bias by over-adjusting the Kamchatkan component by 1% and under-adjusting the western Alaskan component by 0.4%, thus increasing the apparent number of Kamchatkan sockeye in the high seas samples for 1957.

The reference samples used in the scale studies include sockeye from the major sockeye stocks of Kamchatka and western Alaska. However, the sockeye of minor stocks of the Bering Sea rivers (both Asian and North American) not included in the standard samples might not have classified correctly to continent of origin. The effects of this misclassification would not be significant if the fish were mixed at sea with the much larger runs to Kamchatka and western Alaska. However, if they appeared in high seas samples separately from the larger runs, the classificatory results might be highly erroneous. This may account for the large proportion of fish classified as western Alaskan in the 1958 sample at 58°N, 166°E (off northeast Kamchatka).

It is obvious that if the scale studies by Mosher (1963) and Mosher *et al.* (1961) are considered apart from knowledge from other sources, there is no way of determining how well the method identifies the origin of sockeye in the high seas samples. There is no way in the scale studies themselves to support the assumption that the fish in the samples are from only Kamchatka and western Alaska, nor is there any way of testing the implied assumption that Kamchatkan and western Alaskan sockeye each are, on the average, mixed in the high seas samples in the same proportions as in the average of inshore reference samples from Kamchatka or western Alaska. Means of evaluating these assumptions must depend on information from other sources.

The assumption that the maturing sockeye in the high seas samples shown in Table 12 originated in either Kamchatka or western Alaska seems well supported by the results of the tagging and parasite studies.

The adequacy, in general, of the errors of misclassification derived from the inshore standards can be examined by comparing the classification by the bivariate tables of maturing sockeye in high seas samples with the results of parasite and tagging studies. These latter studies have shown that the maturing sockeye taken near southeastern Kamchatka in May and June are essentially of Kamchatkan origin and that the maturing sockeye taken in the eastern Bering Sea in May and June are principally of western Alaskan origin. We note that the three scale samples taken off southeastern Kamchatka west of 168°E (two in 1957 and one in 1958) (Table 12) were classified as more than 96% (adjusted) Kamchatkan. Moreover, the seven samples which were used as empirical tests of the efficiency of the bivariate tables (Mosher, 1963, pp. 49, 51) showed a very high efficiency of classification of Kamchatkan fish, except for one sample from the Kamchatka River in 1956. The error of misclassification for this sample was 34.1%. The 12 samples shown in Table 12 from east of 180° were all classified as 79% or more western Alaskan. Examination of the results of classifying the samples of known origin leads us to conclude that, in general, the bivariate method of determining the origin of high seas sockeye provided reliable results.

Miscellaneous Scale Studies

Mosher (1963) showed that sockeye of the 5_4, 6_2, 6_4 and older age groups were absent, or present to a low degree, in North American samples except those from Kodiak Island, and that they were common in most Kamchatkan samples. This difference is reflected in the higher proportion of these older age groups of sockeye in high seas samples taken west of 180° than in samples taken east of 180°.

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[8] Although not discussed in the papers by Mosher (1963) and Mosher *et al.* (1961), data made available to us indicate differences in the errors of misclassification among the various age categories in the samples used as standards.

Gilbert (1914) appears to have been first to recognize the distinctive pattern of circuli which occurs on the scales of sockeye from Rivers Inlet, British Columbia. Manzer *et al.* (1960) (later published without authorship in INPFC, 1961, pp. 31–32), and Mosher *et al.* (1961) reported the occurrence of Rivers and Smith inlets, British Columbia, type scales in samples taken at sea. Sockeye with this scale pattern were found to be distributed at sea in the waters north of 50°N from British Columbia to 175°W. Figure 3 in INPFC (1961, p. 32) is of particular interest. Of the 44 Rivers and Smith inlets type sockeye shown, the seven immature specimens are distributed farthest from the river of origin. From scale evidence, it appears that sockeye from Rivers and Smith inlets are found at sea more than 1,500 miles to the west, and that immature fish have been found at greater distances than maturing individuals.

Evidence from Serology

Four types of serological or immunochemical studies have been pursued in a search for differences between stocks of sockeye which could be used to recognize the origin of sockeye taken on the high seas. These studies concerned research on haemoglobin antigens, erythrocyte (cellular) antigens, soluble tissue antigens and soluble serum antigens.

Haemoglobin Antigens

In studies on haemoglobin antigens, using the antiserum absorption method (anti-sera were produced in rabbits) in combination with the precipitation ring test, Japanese workers (INPFC, 1959, pp. 61–63) reported the existence of differences between the haemoglobin fraction of the blood of sockeye taken in different oceanic areas.

While the results of these studies show that intraspecific differences occur in the antigenic structure of sockeye haemoglobin, it is not possible to draw conclusions regarding the origin of the high seas samples examined, primarily because the antigenic characteristics of the haemoglobin in North American stocks have not been studied. Further knowledge of the haemoglobin antigens of Asian sockeye stocks is also required.

One serious technical difficulty which must be overcome before this technique can be applied to a large number of samples is the inability to preserve for long periods of time the erythrocytes from which the haemoglobin is obtained.

Erythrocyte Antigens

The existence of intraspecific antigenic differences in the erythrocytes of sockeye salmon has been demonstrated in several ways. These antigenic differences in erythrocytes are known as blood types. The frequency of various blood types has been shown to differ between populations of sockeye from several different North American areas.

The reagents which were used to detect such differences between stocks of sockeye were (a) natural antibodies (agglutinins) occurring in the sera of some animals, especially pigs, (b) heteroimmune anti-sockeye erythrocyte sera, (c) isoimmune anti-sera and (d) natural antibodies (phytoagglutinins) occurring in extracts from various plants, especially from *Cytisus scoparius* bark (Ridgway *et al.*, 1961 ; Ridgway and Klontz, 1961 ; Ridgway and Utter, 1963). The reaction between the reagents and the erythrocytes results in agglutination of the cells.

These techniques have not yet been applied to the problem of recognizing the origin of sockeye taken on the high seas because of the difficulties in obtaining fresh blood, with intact erythrocytes, from Asian and high seas areas. At the present time techniques for preserving the red blood cells intact for considerable periods of time have not been perfected.

Soluble Tissue Antigens

Ridgway (1961) reported on the search for intraspecific differences in the soluble tissue antigens of sockeye and concluded that, " this approach does not appear to offer much promise for racial identification, at least at its present state of development ". Zaks and Sokolova (1961 a, b), on the other hand, studying four different stocks of Kamchatkan sockeye, concluded that there were differences in the antigenic characteristics of muscle extracts.

Soluble Serum Antigens

A modification of Ouchterlony's technique of double diffusion precipitin analysis was used by Ridgway *et al.* (1962) to investigate differences in soluble serum antigens of sockeye of different origins. The anti-sera used in these studies were produced in rabbits.

From sampling carried out from 1955 to 1958, inclusive, these authors reported the occurrence of one or both of two antigens (referred to as antigens I and II) in the serum of 96.8% of 955 sockeye from North American areas from the Columbia River north to western Alaska, and the absence of these two antigens from 92.1% of 126 sockeye from the Sea of

Okhotsk and the east coast of Kamchatka. Because of their proximity to Kamchatka, the latter samples were considered to consist of sockeye of Kamchatkan origin and were used as Kamchatkan standards for comparison with samples from mid-ocean areas. Samples from Kamchatkan rivers were not available.

According to Ridgway *et al.* (1962), antigens I and II were found to be independent of sex and state of maturity, except that they were lost sometime between one week before spawning and death.

The sera of several hundred sockeye taken on the high seas in 1957 and 1958 were examined for the presence of antigens I and II. From the results presented by Ridgway *et al.* (1962) it would appear that Kamchatkan and North American sockeye were about equally represented in the samples taken between 172°E and 169°W in the Bering Sea and between 173°E and 165°W in the North Pacific Ocean. There were no east-west gradations in the relative proportions of North American and Kamchatkan sockeye in the samples; the proportions of Kamchatkan sockeye were as high (approximately 50%) in the samples from the easternmost longitudes as in those from the westernmost longitudes. These results are inconsistent with those obtained from other lines of research, especially in that the proportions of North American sockeye in the samples from the more easterly longitudes are too low.

Apparently there is some inherent difficulty in applying Ridgway *et al.*'s (1962) methods to the problem of recognizing the origin of sockeye taken on the high seas, and until this difficulty is overcome the method cannot be used to this end. This was recognized by Ridgway (1961) and Ridgway and Utter (1963). The possibility that the methods of collection and preservation of blood samples aboard fishing vessels may destroy the antigens or inhibit the antigen-antibody reaction was given considerable attention by these authors, but as yet a solution to the problem has not been found. Another problem involved in these studies, and to which these authors have also devoted considerable effort, is the difficulty in consistently producing potent and specific anti-sera for the detection of antigens I and II in sockeye sera.

The fact that it has not been possible to demonstrate the presence of antigens I or II in the sera of many apparently North American sockeye taken on the high seas poses the question of whether the basic premise that antigens I or II are absent from almost all Kamchatkan sockeye is valid. The sockeye used as Asian standards were taken off the west and east coasts of Kamchatka, and serum samples from these fish were collected aboard commercial fishing vessels or research vessels and probably were subjected to the same treatment as the serum samples taken from sockeye aboard research vessels in eastern and mid-ocean areas. Thus, the problems associated with the collection and preservation of serum samples aboard ship, which may be responsible for the failure to detect antigens I or II in fish caught by research vessels in eastern and mid-ocean areas, may equally apply to the serum samples taken in the far western areas (including the Okhotsk Sea), and which were used as Asian standards. Hence, the proportion of sockeye of Asian origin which possesses antigens I or II or both may be higher than was indicated by Ridgway *et al.* (1962).

Zaks and Sokolova (1961 a, b) have shown by precipitation reactions that the antigenic properties of the blood sera of four stocks of Kamchatkan sockeye differ, but their work has not been extended to investigate the major Asian stocks.

DISCUSSION

In the preceding sections of this paper we have assessed the evidence and summarized the results from individual lines of investigation concerning the origins of sockeye taken at sea in the years 1955 to 1962. These investigations were carried out principally during the five-month period from April through August. However, some features of the distribution and movements of fish at other times of the year may be inferred from their known distribution and movements in the summer months of one year and in the spring months of the following year. There have been some recent surveys of the winter distribution of sockeye salmon (French, 1964, 1966; French and Mason, 1964; INPFC, 1964 b, pp. 40–41) but, with a few exceptions in the Gulf of Alaska, the origins of the fish caught have not been identified.

In the present section we shall combine the results of all investigations to consider the oceanic distribution and migrations of sockeye stocks originating in the three main geographic regions—Kamchatka, western Alaska or Bristol Bay, and the North American rivers tributary to the northeast Pacific (including the Gulf of Alaska)—and finally to discuss intermingling of the many stocks.

Distribution and Migrations of Kamchatkan Sockeye

Maturing Sockeye

The results of parasitological studies (Fig. 59) and inshore or stream recoveries of fish tagged on the high seas (Figs. 19 and 20) have shown that in spring and early summer maturing Kamchatkan sockeye have occurred eastward to 175°E in the Bering Sea and to 173°30′E in the North Pacific Ocean, and from latitudes 47°N to 58°N. The tagging results also have indicated that maturing east Kamchatkan sockeye were distributed farther north than maturing west Kamchatkan sockeye (compare Figs. 19 and 20).

The eastward limit of distribution of maturing Kamchatkan sockeye, especially in the North Pacific Ocean, almost certainly extends beyond that just described. As noted in the section on tagging, high seas recoveries by the Japanese mothership fishery in the western Pacific of fish tagged south of the Aleutians indicated that maturing Kamchatkan sockeye probably occurred, at least in some years, as far east as about 177°W in the spring, and possibly even as far east as 159°W in more southerly waters in early spring. Based on the same evidence the southern limit extends to at least 44°N between 160°E and 170°E.

The results of the morphological studies also suggested the presence of maturing Kamchatkan sockeye south of the central Aleutians in May and June. Further, the morphological and scale studies suggested the presence of maturing Kamchatkan sockeye at least as far east as 180° to 175°W in the Bering Sea in June in some years, and northward to 60°N in the vicinity of 170°E.

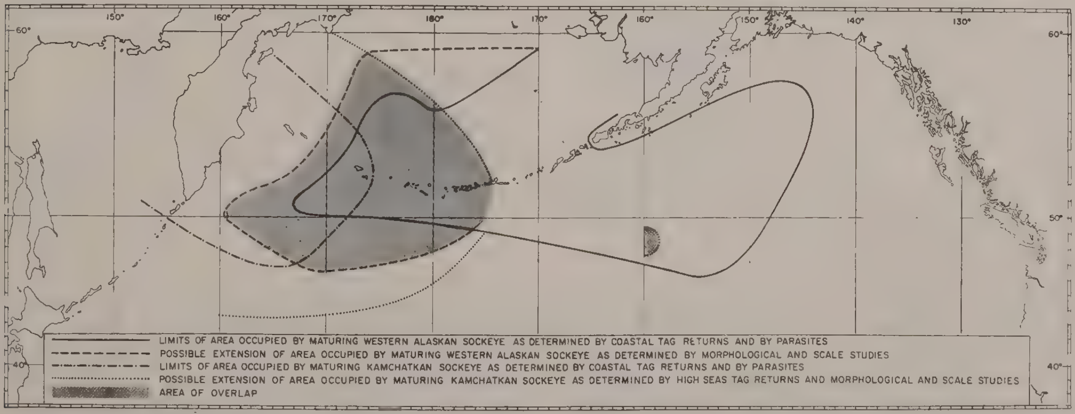
The general area of distribution of maturing Kamchatkan sockeye is shown in Figure 74.

Precise eastern limits of distribution of Kamchatkan sockeye could not be determined by the use of morphological or scale characters because of the limitations inherent in the methods, as already described. Firstly, the procedures for identification allowed only for a fish to be assigned to Kamchatka or to western Alaska. North American sockeye having originated in areas other than western Alaska would be misclassified either as Kamchatkan or western Alaskan. In the morphological studies such sockeye would be largely misclassified as Kamchatkan (Fukuhara *et al.*, 1962). The effect of this type of misclassification on interpretation of the morphological results has been discussed in the review of the morphological studies. Secondly, even if only Kamchatkan or western Alaskan sockeye were present in the samples being classified (as probably was the case in many instances), it would not be possible to identify with certainty the origin of individual sockeye because of an overlap in the morphological and scale characteristics of Kamchatkan and western Alaskan fish.

The lack of direct evidence, based on the presence of the parasite *Dacnitis truttae* or on recoveries of tagged fish in inshore waters, of the occurrence of maturing Kamchatkan sockeye east of about 175°E may be regarded as a sampling problem and can be explained as follows.

As described earlier, only about 1%–2% of Kamchatkan sockeye as a whole appear to be infected with *D. truttae*. With increased dilution of Kamchatkan sockeye with those of other origins on the high seas, the incidence of infection with this parasite in high seas samples decreases. Consequently, in the Aleutian area of the North Pacific Ocean, where Bristol Bay maturing sockeye are generally predominant, the probability of encountering a *Dacnitis*-infected maturing Kamchatkan sockeye in the samples examined (see Figs. 54 to 58) would, indeed, be very low. The absence of *D. truttae* from these Aleutian samples, therefore, must not be taken as indicative of the absence of Kamchatkan sockeye.

Taggings of maturing sockeye in the western and central Aleutians, as described earlier, provided only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LIMITS OF AREA OCCUPIED BY MATURING WESTERN ALASKAN SOCKEYE AS DETERMINED BY COASTAL TAG RETURNS AND BY PARASITES
POSSIBLE EXTENSION OF AREA OCCUPIED BY MATURING WESTERN ALASKAN SOCKEYE AS DETERMINED BY MORPHOLOGICAL AND SCALE STUDIES
LIMITS OF AREA OCCUPIED BY MATURING KAMCHATKAN SOCKEYE AS DETERMINED BY COASTAL TAG RETURNS AND BY PARASITES
POSSIBLE EXTENSION OF AREA OCCUPIED BY MATURING KAMCHATKAN SOCKEYE AS DETERMINED BY HIGH SEAS TAG RETURNS AND MORPHOLOGICAL AND SCALE STUDIES
AREA OF OVERLAP

FIGURE 74. Range of western Alaskan and Kamchatkan maturing sockeye salmon, and area of overlap.

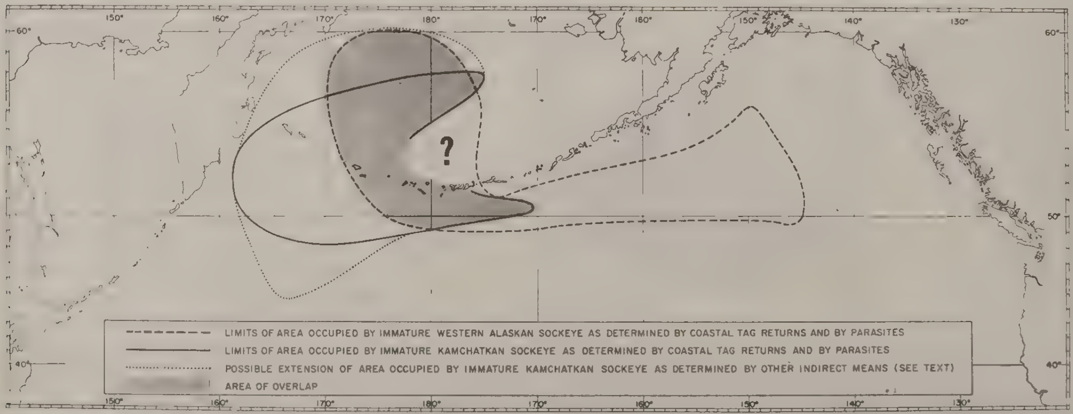
a few high seas recoveries which could be considered almost certainly to be sockeye destined for Kamchatkan streams. On the other hand, during the years 1958–62 numerous high seas recoveries of maturing sockeye presumably destined for Kamchatka were made from fish tagged and released in the waters west of 170°E off southeastern Kamchatka (Figs. 38 to 42). In contrast to the large number of high seas recoveries of apparently Kamchatkan sockeye from these latter tagging operations, only 16 recoveries were made in Kamchatkan streams from these same taggings. It is evident that the proportion of reported recoveries of tagged Kamchatkan sockeye is much greater in the Japanese high seas fishery off the southeast coast of Kamchatka than in the coastal fisheries or streams of Kamchatka. Thus, since the number of recoveries of presumably Kamchatkan sockeye made by the Japanese mothership fishery in waters off southeastern Kamchatka from taggings in the area south of the central Aleutians was small, the lack of Kamchatkan coastal recoveries from the same taggings is insufficient grounds for declaring that maturing Kamchatkan sockeye do not range as far east in the North Pacific Ocean as the central Aleutians.

The migratory patterns of maturing Kamchatkan sockeye are only partly known. Tag recoveries indicate that in the waters to the southwest of the western Aleutians and to the southeast of Kamchatka, as far south as at least 44°N, the main body of maturing Kamchatkan sockeye apparently is present as early as late April and that in general these sockeye move progressively north and west through the months of May, June and July. Those fish destined for west Kamchatka must proceed through the passes of the Kuril Islands, and probably do not migrate as far northward as those sockeye destined for east Kamchatkan streams, particularly those north of about 55°N. Tagging also has strongly suggested that some maturing Kamchatkan sockeye migrate westward in the North Pacific from as far east as the central Aleutians in June and possibly from farther east at more southerly latitudes earlier in the spring. The occurrence of maturing Kamchatkan sockeye in the central and west-central Bering Sea in June, as is indicated by the morphological and scale studies, suggests that there is a westward migration in the Bering Sea towards Kamchatka.

To what extent the migratory patterns of the stocks from east and west Kamchatka, particularly those of the two principal stocks (the Ozernaia River on the southwest coast and the Kamchatka River on the middle east coast), resemble or differ from one another is not known. Aside from any possible differences in routes of migration, there may be a difference in the time of departure from the general offshore feeding area because the east Kamchatkan runs, in general, arrive at their rivers earlier than the west Kamchatkan runs. In particular, the peak period of the Kamchatka River sockeye runs passing through the estuary is about five weeks earlier than that of the runs to the Ozernaia River (Fig. 2).

Immature Sockeye

According to the parasitological results, immature Kamchatkan sockeye have been found eastward to 170°W in the North Pacific Ocean; the southern limit was at 48°N in the western Pacific and at 51°N in the Aleutian area. In the Bering Sea they have been found widely scattered as far east as 175°W and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LIMITS OF AREA OCCUPIED BY IMMATURE WESTERN ALASKAN SOCKEYE AS DETERMINED BY COASTAL TAG RETURNS AND BY PARASITES
LIMITS OF AREA OCCUPIED BY IMMATURE KAMCHATKAN SOCKEYE AS DETERMINED BY COASTAL TAG RETURNS AND BY PARASITES
POSSIBLE EXTENSION OF AREA OCCUPIED BY IMMATURE KAMCHATKAN SOCKEYE AS DETERMINED BY OTHER INDIRECT MEANS (SEE TEXT)
AREA OF OVERLAP

FIGURE 75. Range of one-ocean-winter and older western Alaskan and Kamchatkan immature sockeye salmon, and area of overlap.

northward to 58°N. The known distribution of immature Kamchatkan sockeye is shown in Figure 75.

Tag recoveries in Kamchatkan coastal waters, of which there were only three (tagging locations were about 52°N, 164°E ; 52°30′N, 172°30′E ; and 51°30′N, 176°30′W), do not alter the limits of distribution as defined by parasites. Indirect evidence from high seas recoveries of maturing sockeye tagged as immatures one or two years prior to recovery does not change the eastern or northern limits, but the recovery of a fish tagged by Japan at about 44°N, 167°E in 1959 and recovered at about 51°30′N, 166°E in 1960 (Fig. 51) probably indicates a southern extension of the distribution of immature sockeye to about 44°N.

For the same reasons as discussed for maturing sockeye, the morphological results do not define limits of distribution of immatures. The morphological studies reported herein indicate that immature Kamchatkan sockeye occurred eastward in the Bering Sea to at least about 180°, and in the North Pacific it appeared that they were regularly present at least as far as the central Aleutians.

This wide distribution of immature Kamchatkan sockeye was found in the month of July. Of 20 fish identified by parasites, 13 were caught in July (see Tables XIII-XVI of Margolis, 1963) and two of the three recoveries in Kamchatka of fish tagged as immatures were from tagging in early July. However, apparently they were also widely dispersed in August, a *Dacnitis*-infected sockeye having been captured off the east coast of Kamchatka, another in the west-central Bering Sea and a third in waters immediately south of the mid-Aleutians. The five immature Kamchatkan sockeye caught between late May and late June (identified by parasites or by tagging) were confined to the area between about 172°30′E and 167°30′E, and 48°N and 52°30′N. Their distribution during this period, however, may well extend farther eastward in the North Pacific Ocean, judging from the high seas recovery at about 53°30′N, 163°E (Fig. 53 a) on July 3, 1959, of a maturing sockeye which was tagged two years previously (apparently as a two-ocean-winter fish) at about 51°30′N, 176°30′W on June 13 ; based on locality and date of recapture this fish was most likely destined for a Kamchatkan river.

The parasitological data indicate that the main concentrations of immature Kamchatkan sockeye occur west of 175°E. Although many fewer immature sockeye from west of 175°E than from 175°E and eastward were examined for parasites, three times as many *Dacnitis*-infected immatures were found in the samples from west of 175°E than in the more easterly samples (see Figs. 60–63).

The migrations or movements of immature Kamchatkan sockeye can only be partially reconstructed from available information ; much remains unknown.

The direction of movement of the immature Kamchatkan sockeye found south of the Aleutians can be inferred from evidence of direction of movement provided by purse seine catches, as described earlier. Since the movement of sockeye along the south side of the Aleutians is markedly in a westerly direction, it must be concluded that, in general, the immature Kamchatkan sockeye caught in this area in the summer were also moving westward. This would imply that the easterly migration from Kamchatka took place during an earlier period, and probably well to the south of the Aleutians because immature sockeye are relatively scarce close to the Aleutians prior to the latter part of June.

Some of the immature Kamchatkan sockeye found immediately south and north of the central Aleutians in July and August were of the one-ocean-winter age, as seen from the results of the parasitological (discussed previously) and morphological studies. Some of the samples from the central Aleutian area used in the morphological studies, and from which the classificatory results presented in Table 10 were obtained, consisted predominantly of one-ocean-winter fish (unpublished data on file at the U.S. Fish and Wildlife Service Laboratory, Seattle ; also see Manzer *et al.*, 1965, Appendix Table B, for age composition of catches in the Aleutian area by United States research vessels). Thus, although the paths of migration are unknown, it is apparent that within a little more than one year of leaving their rivers of origin some Kamchatkan sockeye migrate eastward as much as 1,000 miles.

In the waters of the North Pacific and Bering Sea west of about 170°E, according to changes of abundance with respect to time and latitude, there is a general northward movement of immature sockeye of all ages from May through August (Manzer *et al.*, 1965). Recoveries a year later from tagging experiments conducted in July and August in the waters west of about 170°E and between 52°N and 58°N (mainly 52°–55°N) indicated a general southerly migration in the fall or winter or both. The results of the morphological studies (Table 10) and, as just noted, of the parasitological studies indicated that these immature salmon west of about 170°E are mainly of Kamchatkan origin. Thus, in the spring and summer some portion of the immature Kamchatkan sockeye in western Pacific waters migrate northward into the western Bering Sea and in the fall or winter or both there is a return migration to more southerly waters.

Some, however, may winter in the Bering Sea. Recent winter fishing operations by a research vessel, along 175°E and 180° as far north as 57°30′N, have indicated the presence of significant numbers of sockeye in late January and early February (French and Mason, 1964).

It is also possible that the source of some of the immature Kamchatkan sockeye observed in the summer in the Bering Sea west of 170°E was the westward moving fish along the south side of the central Aleutians, since an immature sockeye tagged at about 51°30′N, 176°30′W on June 14, 1963, was recovered in the same year in the western Bering Sea at about 59°N, 167°E on July 23 (Hartt and Dell, 1964 ; the dates of tagging and recovery were obtained by personal communication).

The routes by which immature Kamchatkan sockeye reach the central Bering Sea are not definitely known. They may pass from the North Pacific through the Aleutian passes or move eastward from the western Bering Sea.

Distribution and Migrations of Western Alaskan (chiefly Bristol Bay) Sockeye

Maturing Sockeye

Numerous inshore or stream recoveries of tagged fish within the year of tagging (Fig. 21) and the occurrence of *Triaenophorus*-infected maturing sockeye in high seas samples (Fig. 59) have demonstrated an exceedingly vast distribution of maturing western Alaskan (chiefly Bristol Bay) sockeye in the North Pacific Ocean and the Bering Sea. The complete east-west range in the North Pacific extended from 167°E to 142°30′W and in the Bering Sea it extended westward to 171°E. The known southern limit of distribution varied according to the longitude. It was about 50°N near the western extremity of the range (168°E), 49°N south of the central Aleutians (173°30′W), 48°N south of the eastern Aleutians (166°W) and 46°N in the western Gulf of Alaska (155°W). Eastward from 155°W tag recoveries indicated that the southern boundary shifted progressively northward ; at 142°30′W it was 56°N. The most northerly distribution determined for maturing Bristol Bay sockeye in the Gulf of Alaska was at 58°N (at 145°W), according to parasitological results. In the Bering Sea, the northern limits at the western end of the range were somewhat farther south than those at the eastern end. The most northerly latitude of Bristol Bay sockeye distribution in the Bering Sea was 59°N (at 170°W) ; it was 58°N at 174°W, 57°N at 180°, 58°N at 176°E, 57°N at 173°E, and 55°N at 171°E.

The more southerly distribution of maturing Bristol Bay sockeye determined by tagging and the more extensive distribution in the central and west-central Bering Sea determined by parasitology are due to differences between the areas in which tagged sockeye were released and the areas from which samples were examined for parasites (compare Figs. 5, 6, 9 and 10 with Figs. 54 to 58).

Many tagged maturing sockeye, apparently destined for Bristol Bay, were recovered on the high seas, especially in the Bering Sea. Their positions of release fall within the ocean range of Bristol Bay maturing sockeye just described.

Results of the morphological and scale studies cannot be used to define extreme limits of distribution of Bristol Bay sockeye. However, in general, the results of these studies are in keeping with those of tagging and parasitology, although they suggest a possible westward extension to about 160°E in the vicinity of 50°N and a possible southern extension to about 47°N near 168°E.

The general area of distribution of maturing Bristol Bay sockeye is shown in Figure 74.

Some aspects of the migrations of maturing Bristol Bay sockeye can be reconstructed from evidence provided by tag recoveries and direction of movement determined by purse seine fishing. Some supplementary information is available from parasitological results.

Tagging operations in late April and in May have revealed the presence of what may be the main concentration of maturing Bristol Bay sockeye in mid-spring in the area well to the south of the Alaska Peninsula and extending into the central Gulf of Alaska. Apparently there also is a westward extension of these maturing fish, the limit of which is not known prior to mid-May. The occurrence of maturing Bristol Bay sockeye, as determined by parasites in 1958 and by tagging in 1961, just north of 50°N and west of 170°E in mid-May and early June suggests that the wintering range extends well to the west. From their wintering areas in the eastern North Pacific they move northward, westward or northwestward towards the Bering Sea. Upon reaching the Alaska Peninsula and Aleutian Islands they continue in a westerly direction or turn westward (depending on their prior movement), subsequently moving into the Bering Sea through the Aleutian passes. For sockeye which wintered to the southwest of the Aleutians, movement into the Bering Sea may occur between the Aleutians and the Komandorski Islands. The relative importance of various passes into the Bering Sea varies between years, such variation significantly affecting the distribution of maturing Bristol Bay sockeye in the Bering Sea.

After entry into the Bering Sea, eastward movement to Bristol Bay is preceded in many cases by considerable northward dispersal, judging from the high seas recoveries of fish tagged south of the Aleutians and from the results of parasitology and morphology, which indicate a wide dispersal of maturing Bristol Bay sockeye in the Bering Sea. It is also possible that some of the maturing Bristol Bay sockeye found in the Bering Sea in spring had wintered there, since fishing in late January and early February in the west-central Bering Sea has indicated the presence of maturing sockeye at that time. However, it must be borne in mind that the sockeye present in the Bering Sea in early February could migrate southward out of the Bering Sea prior to May.

The timing of the migration is such that maturing Bristol Bay sockeye do not appear in numbers in the waters immediately south of the Aleutians until the latter part of May and their numbers in this area decrease markedly towards the end of June. The migration from the Gulf of Alaska lasts until about mid-June ; no recoveries of maturing sockeye tagged in the Gulf after June 17 have been made in Bristol Bay, nor have any *Triaenophorus*-infected maturing sockeye been caught in the Gulf later than June 15. The timing of the disappearance of maturing Bristol Bay sockeye from the area just to the southwest of Attu Island (westernmost of the Aleutian Islands) appears to be early June. No recoveries have been made in Bristol Bay of fish tagged immediately to the south or southwest of Attu Island later than June 8, nor have any sockeye infected with *Triaenophorus* been observed in samples taken in this area later than June 8. The migration into Bristol Bay from the Bering Sea occurs principally during June. The above-described timing of the Bristol Bay migration is associated with the consistent appearance of sockeye in the estuaries in numbers commencing in the third week of June and reaching a peak during the week of July 3–10 ; the runs decline to very low levels after July.

Although the main body of maturing Bristol Bay sockeye has vacated oceanic areas by the end of June, tagging and parasitological results have indicated that some may still be found south of the Aleutians or in the Bering Sea (as far west as 173°E) in early July. Furthermore, parasitological results have indicated that some may not yet have entered the Bering Sea by early August ; in each of 1958 and 1959 a *Triaenophorus*-infected maturing sockeye was found in samples from south of the mid-Aleutians (175°W) on August 5. Although some maturing Bristol Bay sockeye may have been tagged in late July or early August, recoveries from such taggings would not be likely because the commercial fishery, on which recoveries are largely dependent, terminates in late July.

Immature Sockeye

The distribution of immature Bristol Bay sockeye has been shown best by parasitological studies (Fig. 64). Tagging, of course, has also given much direct evidence of their distribution but the recoveries (Figs. 43 and 44) have been from taggings in relatively restricted areas.

The evidence from both studies combined shows the known range in the North Pacific to be from 172°E in the west to 145°W in the east, with a southern limit of 49°N to 50°N ; they occur northward to at least 56°N in the western Gulf of Alaska (at 150°W) and to the Aleutian Islands farther westward. In the Bering Sea, immature Bristol Bay sockeye have been found from the Aleutians to as far north as 60°N, and between 170°E and 175°W. The known distribution of immature Bristol Bay sockeye having spent one or more winters at sea is shown in Figure 75.

High seas recoveries of maturing fish which were tagged when immature and which could reasonably be considered to be of Bristol Bay origin do not extend the known range just described for immature sockeye, nor do the morphological studies reported earlier.

This broad distribution of immature Bristol Bay sockeye was observed generally in late June, July and August, according to tag recovery data given by Hartt (1966) and parasitological data presented by Margolis (1963). Little evidence is available on their distribution earlier in the year. One immature Bristol Bay sockeye was identified by tagging in early June south of the mid-Aleutians (about 51°30′N, 176°30′W) and one by parasites about mid-May from the south-central Gulf of Alaska (50°N, 145°W).

The distribution revealed by tagging (according to data presented by Hartt, 1966), by parasitology and by morphology, of one-ocean-winter Bristol Bay sockeye, shows that within a little more than one year of leaving their rivers of origin Bristol Bay sockeye may migrate westward about 1,100 to 1,200 miles (to 173°30′E south of the Aleutians), or about as far westward as older fish.

The migratory patterns of immature Bristol Bay sockeye are only partly known. Purse seine fishing (Hartt, 1962, 1966) and gillnet fishing (Manzer *et al.*, 1965) have shown immature sockeye to be relatively scarce immediately south of the Aleutian area prior to late June. The appearance of these fish, which include Bristol Bay immatures, in the Aleutian area in late June suggests that they have migrated northward from farther south and southeast (and possibly also southwest) of the Aleutians, similar to the migration of maturing Bristol Bay sockeye described earlier, but at a somewhat later date. Since the immature sockeye occurring south of the Aleutians in the summer were moving predominantly westward, those of Bristol Bay origin must also have been moving predominantly in this direction. The recovery in the western Bering Sea (59°N, 167°E) of an immature sockeye tagged in the same year immediately south of the central Aleutians suggests that some of the westward moving immature Bristol Bay sockeye may migrate into the western Bering Sea to contribute to the large concentrations of immature sockeye observed there in July and August. The immature Bristol Bay sockeye observed in the south-central Bering Sea probably migrated there through the Aleutian passes ; those found in the more northern parts of the central Bering Sea may also have come directly northward from south of the Aleutians or may have migrated eastward from the western Bering Sea.

Because concentrations of maturing Bristol Bay sockeye occur in mid-spring in the west-central Gulf of Alaska and in the northeast Pacific well to the south of the Alaska Peninsula, with a westward extension to at least about 170°E, the immature fish occurring along the Aleutians and in the western Bering Sea in the previous August (Fig. 3) must have undertaken, in part, a southward and, in part, an eastward migration, with a northeastward migration into the Gulf of Alaska, between September and April. Those fish which would be remaining another year at sea as immatures seem also to undergo this general southward migration in the winter. However, from results mentioned earlier of winter fishing in the Bering Sea it is possible that some Bristol Bay immatures winter in the Bering Sea, whether or not they will be maturing the following summer.

DISTRIBUTION AND MIGRATIONS OF SOCKEYE FROM NORTH AMERICAN RIVERS TRIBUTARY TO THE NORTHEAST PACIFIC (INCLUDING THE GULF OF ALASKA)

With one exception information regarding high seas distribution and migrations of sockeye from these rivers has been obtained from tagging experiments. Some information on Smith Inlet and Rivers Inlet (British Columbia) sockeye has been obtained from scale studies.

Maturing Sockeye

The known limits of distribution determined by tagging for the various stocks from the Chignik River on the south side of the Alaska Peninsula eastward and southward to the Columbia River have been given in Table 6. The maturing fish of these stocks are chiefly found east of 160°W, but individuals of some of these stocks (Chignik River, Kodiak Island, Cook Inlet and Nass River) have been found in the waters south of the Aleutians, in two cases as far west as about 176°30′W (Figs. 22 to 30).

The high seas range of maturing Rivers Inlet and Smith Inlet sockeye determined from scale studies falls within that determined by tagging.

The migrations of maturing "northeast Pacific" sockeye may be inferred from their distributions at sea in the spring and early summer months. The sockeye found south of the Aleutians must undergo a considerable eastward migration to reach their rivers of origin. However, the main high seas concentration of these sockeye lies within the Gulf of Alaska, and their homeward migration must take place in different directions for different stocks. The stocks from the northern rim of the Gulf must move northward, northwestward or northeastward ; those from the more southerly and easterly areas must move eastward, southeastward or northeastward. There is some evidence from tagging that the stocks from the more southerly areas migrate some distance to the north in the spring before returning south and east towards their rivers of origin.

Tagging showed that all the principal stocks were present in the Gulf of Alaska from April to July. However, the main body of certain stocks moves coastward earlier than others. For example, most of the recovered Copper River sockeye were tagged prior to June and most of the Cook Inlet recoveries had been tagged prior to July, whereas as many of the fish recovered in southeastern Alaska to southern British Columbia were tagged in July as were tagged in May or June.

Immature Sockeye

Although it seems likely that the main body of immature sockeye from North American rivers tributary to the northeast Pacific occurs within the Gulf of Alaska, there have been too few recoveries of maturing sockeye tagged as immatures to enable a description of the limits of distribution of the various stocks. Up to 1962 there were only six sockeye recovered one or two years after tagging. Two of these indicate, however, a considerable westward migration : a sockeye recovered in southeastern Alaska was tagged a year earlier at 176°30′W and one recovered in Rivers Inlet was tagged two years earlier at 177°30′E, both immediately south of the Aleutians.

The distribution determined by scale studies for immature Rivers Inlet and Smith Inlet sockeye does not extend as far westward as that indicated by the tag recovery just mentioned.

INTERMINGLING OF SOCKEYE STOCKS

East and West Kamchatka

Information on intermingling of sockeye from east and west Kamchatka is available only from tagging results. The few recoveries in east and west Kamchatka of tagged maturing sockeye (Figs. 19 and 20) show that stocks from both these regions overlap in their distributions west of 170°E between approximately 48°N and 52°N. Actual intermingling of maturing east and west Kamchatkan sockeye, in the sense of occurring at the same place at the same time, has been demonstrated only in the area between about 164°30′E and 165°E, and between 50°30′N and 52°N, in early July of 1958.

Tagging has not contributed any information on intermingling of immature sockeye from east and west Kamchatka, since only three recoveries have been made in Kamchatka of fish tagged as immatures—two in east Kamchatka and one from an unknown locality.

Better means of distinguishing between sockeye of east and west Kamchatkan origins is required to define adequately the ocean areas of overlap in distribution and intermingling of sockeye from these two regions.

Kamchatka and Western Alaska (chiefly Bristol Bay)

Maturing sockeye. From the descriptions of the distribution of Bristol Bay and Kamchatkan sockeye it is apparent that there are areas in the North Pacific Ocean and in the Bering Sea in which maturing sockeye from both these regions occur during the spring months. Information obtained up to and including 1962 on coastal or stream recoveries of tagged fish (Figs. 19, 20 and 21) and on the distribution of individual fish identified by the presence of a characteristic parasite (Fig. 59) indicates that the area of overlap was not extensive; it lay between 167°E and 173°30′E in North Pacific waters north of 50°N, and between 171°E and 175°E south of 55°N in the Bering Sea. When information from morphological and and scale studies and from high seas tag recoveries is taken into consideration it is apparent that the area of overlap probably is much broader. However, its exact limits cannot be defined. It probably extends eastward to about the mid-Aleutian area, and in waters south of 50°N even to as far east as 159°W; it possibly extends westward to about 160°E and probably northward in the west-central Bering Sea to about 59°N, and southward in the North Pacific to about 47°N in the vicinity of 168°E. The approximate area of overlap of maturing Bristol Bay and Kamchatkan sockeye, taking into consideration indirect evidence, lies between about 160°E and 159°W, as is shown in Figure 74. However, the principal area of overlap, as will be noted below, probably lies between about 170°E and about 180°, north of about 48° or 49°N. The results from morphology and scale studies suggest that this main area of overlap is also the main area of actual intermingling, in that fish of both Kamchatkan and western Alaskan origins occur at the same place at the same time.

From the results of morphological, scale and parasitological studies, and from tag recoveries, it is possible to provide a general description of the oceanic areas dominated by maturing western Alaskan or Kamchatkan sockeye in the months of May and June. The areas from which samples were obtained for the morphological, scale and parasitological studies, and the areas in which fish were tagged, were not necessarily identical for any given year, and the areas of coverage were not identical from year to year. Nevertheless, the following generalizations appear to apply.

In the North Pacific Ocean from 1956 to 1961, during May and June, maturing western Alaskan sockeye dominated westward to about 180° and maturing Kamchatkan sockeye dominated eastward to about 172°–173°E. Sampling between 173°E and 180° was irregular but dominance appeared to vary both within and between years, especially from 50°N to the Aleutian Islands; limited sampling south of 50°N indicated predominance of Kamchatkan sockeye eastward to 175°E.

In the Bering Sea during the same months in these same years, with the exception of 1958, western Alaskan sockeye dominated to about 180°. Sampling was sparse west of 180°, but the few available samples indicate that Kamchatkan sockeye dominated west of about 174°E. In 1958 the parasitological studies indicated that the western limit of dominance of maturing Bristol Bay sockeye lay between 170°W and 180°. (No scale or morphological data were available for the area between 172°30′W and 180°, and tagging was not conducted west of 174°W.) The abundance

TABLE 13. Commercial catch and escapement of sockeye salmon in Bristol Bay, Alaska, 1956–61 (in millions of fish).

Year	Catch[1]	Escapement[2]	Total[3]
1956	8.88	14.64	23.52
1957	6.28	4.83	11.11
1958	2.99	2.86	5.85
1959	4.61	8.06	12.67
1960	13.71	21.13	34.84
1961	11.91	5.97	17.88

[1] From Table 52 of Kasahara (1963).

[2] From Table 77 of Kasahara (1963).

[3] The minor differences between the numbers given in this table and those given in Table 11 for the total stock size in the years 1956–59 occurred in the data sources used.

of maturing sockeye salmon in the central and eastern Bering Sea was relatively low in 1958 (Manzer *et al.*, 1965) and the returning sockeye runs to Bristol Bay were relatively small (Table 13). The apparent difference between 1958 and the other years of study in the western limit of dominance of western Alaskan maturing sockeye in the Bering Sea appears to be related to the relatively low abundance of Bristol Bay maturing sockeye in 1958.

Immature sockeye. As was shown for maturing sockeye, there are also broad areas in the North Pacific Ocean and Bering Sea where the distributions of immature Kamchatkan and western Alaskan sockeye overlap. This area of overlap is most apparent during the months of July and August, after most of the maturing fish have migrated coastward.

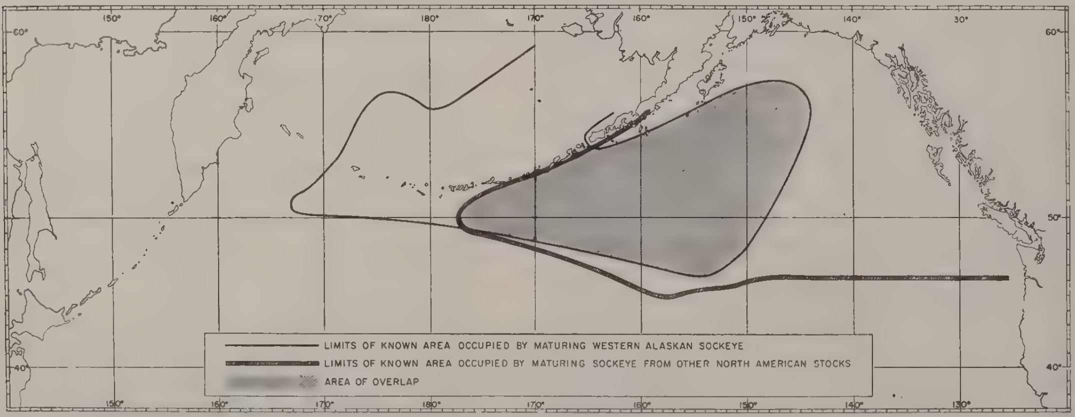
Direct evidence from tag recoveries in coastal waters or streams, and from identification of fish by parasites, indicates an area of overlap in the North Pacific between 172°E and 170°W and in the Bering Sea between about 171°E and 175°W northward to about 58°N. When information on the abundance of immature sockeye in summer in the northeastern Bering Sea is taken into consideration, it appears that the area of overlap in the Bering Sea extends northward to about 60°N, at least west of 180° (Fig. 75) The morphological results suggest that this area of overlap is also the area of intermingling.

Within the area of intermingling in the Bering Sea, data are insufficient to determine the region dominated by either Kamchatkan or Bristol Bay sockeye. In the North Pacific, however, the morphological results suggest that immature Bristol Bay sockeye generally were dominant in 1956, 1957, 1959 and 1960 in the area of intermingling, but that in 1958 Kamchatkan sockeye were dominant in this area.

Bristol Bay and Other North American Stocks

Maturing sockeye. It has been shown earlier, from the results of tagging, that the maturing sockeye of the stocks originating in rivers tributary to the northeast Pacific Ocean occur east of 160°W, for the most part, although individuals of some stocks have been shown to occur westward to the mid-Aleutian area. These North American stocks intermingle extensively in the central portion of the Gulf of Alaska. Since the range of maturing Bristol Bay sockeye also extends eastward into the Gulf of Alaska at the same time as other North American stocks are found there, it is apparent that all major North American sockeye stocks intermingle extensively over a fairly broad area in the Gulf of Alaska. With the migration of sockeye towards their home streams as the spring and summer seasons advance, the extent of intermingling decreases; Bristol Bay sockeye leave the Gulf of Alaska by about mid-June. The extreme western limit of the area of overlap of Bristol Bay sockeye and other North American stocks, in particular those from the Nass and Skeena rivers area and northward, occurs in the mid-Aleutian area. The known area of overlap (which to a large extent is also the area of intermingling) in the distributions of Bristol Bay sockeye and other North American stocks in shown in Figure 76.

Immature sockeye. Because there are so few data available on the oceanic distribution of immature sockeye from streams tributary to the northeast Pacific Ocean, it is not possible to delineate the area of overlap between immature sockeye of these stocks and those from western Alaska. However, since im-


150°
160°
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140°
130°
LIMITS OF KNOWN AREA OCCUPIED BY MATURING WESTERN ALASKAN SOCKEYE
LIMITS OF KNOWN AREA OCCUPIED BY MATURING SOCKEYE FROM OTHER NORTH AMERICAN STOCKS
AREA OF OVERLAP

FIGURE 76. Range of western Alaskan and other North American stocks of maturing sockeye salmon, and area of overlap.

mature Bristol Bay sockeye have been identified in the Gulf of Alaska eastward to 145°W (at 50°N) and south of the Aleutians westward to about 172°E, and since an immature sockeye tagged at 177°30′E immediately south of the Aleutians was recovered in Rivers Inlet and another tagged at 176°30′W was recovered in southeastern Alaska, it is apparent that the oceanic distributions of immature sockeye from western Alaska and of immature sockeye from other North American areas show considerable overlap.

SUMMARY

1. Sockeye salmon spend up to four years (usually one or two) in fresh water before migrating to sea and up to four years (usually two or three) in the sea before returning to their natal waters to spawn. Each sockeye stock has its own characteristic age categories, although the relative proportions of the individual age categories within a stock may show considerable annual variations.

2. Seaward migration occurs during the spring months, mainly from about mid-April to late June, and adult upstream migration takes place mainly from May to October. The timing of the downstream migration of smolts and of the upstream migration of adults varies among the different stocks but is relatively constant from year to year for individual stocks.

3 (a). In Asia, sockeye production is almost entirely limited to the Kamchatka Peninsula of the U.S.S.R. Relatively small numbers are produced in watersheds of the northern Bering Sea and northern Okhotsk Sea coasts. A combined total of approximately 90% of Asian sockeye is produced in the Ozernaia River system and the Kamchatka River system, located on the southwest and middle east coasts, respectively, of the Kamchatka Peninsula.

3 (b). In North America, the largest sockeye stocks occur in the Bristol Bay area of western Alaska and in the Fraser River system, British Columbia. Other North American river systems producing commercially significant quantities of sockeye occur between these two regions.

3 (c). It is recognized that sockeye are considerably more abundant in North America than in Asia. For the 21 years included in the periods 1927–30, 1933–36 and 1940–52, the average commercial catch of North American sockeye was 24.8 million fish and that of Asian sockeye was approximately 8.5 million. Comparison of the catches in other years is not possible, either because of incomplete catch data or because there was a high seas catch of fish which could not be accurately apportioned to continent of origin.

4. The area of oceanic distribution of sockeye encompasses the entire width of the North Pacific Ocean north of about 44°N in the west and about 46°N in the east, and extends into the Bering Sea to north of 60°N. From May through August there is a general northward shift in the southern boundary of about 4° of latitude. In the winter months there is apparently a general southward movement, although some fish winter in the Bering Sea. In May the greatest concentrations of sockeye (principally maturing fish) are found offshore in a band stretching from southwest and south of the Aleutians eastward into the north-central Gulf of Alaska. In late May and in June the areas of maximum concentration of these maturing fish shift to the vicinity of the Aleutians, to the central and eastern Bering Sea, and to the northern Gulf of Alaska. With the departure of maturing sockeye from the high seas in June and July, the immatures, which occur mainly south of the maturing fish in May and June, migrate generally northward and westward. In August the greatest concentrations of immature sockeye are found in the Aleutian area and in the western Bering Sea.

5. The results of the identification of Kamchatkan and Bristol Bay (western Alaskan) sockeye on the high seas during the months of May through August, 1955–62, by tagging, by the presence of characteristic parasites, and by morphological and scale characteristics, may be generalized as follows:

a. Maturing Kamchatkan sockeye occurred in the North Pacific Ocean probably as far east as at least about 175°W in the vicinity of the Aleutians in June, and possibly as far east as approximately 160°W (near 48°N) in early May. In waters west of 170°E they were found as far south as at least 44°N in May. In the Bering Sea they probably occurred eastward to at least 180° and possibly to 175°W in June. The main concentrations occurred in the North Pacific, west of about 170°E–175°E from May through July.

b. Immature Kamchatkan sockeye ranged eastward in the North Pacific Ocean to approximately 170°W immediately south of the Aleutians, and in the Bering Sea to at least 175°W and as far north as about 60°N, in July and August. Near 170°E they occurred southward to about 44°N in May. Like the maturing sockeye, the main concentrations of Kamchatkan immatures occurred west of about 170°E–175°E throughout the months of May to August, inclusive.

c. Maturing Bristol Bay sockeye occurred in the North Pacific Ocean eastward to approximately 142°30′W, near 56°N, and westward to at least about 167°E (possibly to 160°E), near 50°N, in May and early June; in the Bering Sea they occurred westward to about 170°E and northward to 59°N in June.

The main concentrations occurred east of about 175°E-180° in May and June.

d. Immature Bristol Bay sockeye were found in the North Pacific Ocean eastward to 145°W (at 50°N) and westward to about 172°E (near the Aleutians), and in the Bering Sea they occurred between about 170°E and 175°W as far north as about 60°N, principally in July and August.

e. Maturing Bristol Bay and Kamchatkan sockeye overlapped in their distributions, during May and June, in the North Pacific Ocean north of about 47°N from at least 167°E to probably about 175°W, and possibly from about 160°E (near 50°N) to about 159°W (near 48°N) ; in the Bering Sea the area of overlap extended from about 170°E to probably 180° and possibly to about 175°W, and northward to about 59°N (near 175°E). Within this area of overlap, maturing Bristol Bay sockeye dominated in the North Pacific Ocean and Bering Sea (except in 1958) eastward to approximately 180° and maturing Kamchatkan sockeye dominated westward to about 172°E-174°E. Between 173°E-174°E and 180°, dominance appears to have varied both within and between years. In 1958 Bristol Bay sockeye appear not to have dominated as far westward as in other years.

f. The known distribution of immature Bristol Bay and Kamchatkan sockeye overlapped in the North Pacific Ocean between 172°E and 170°W (north of 49°N), and in the Bering Sea between about 170°E and 175°W (as far north as 60°N), in July and August. Data are insufficient to determine areas of dominance in the Bering Sea of either Kamchatkan or Bristol Bay immature sockeye. In the area of overlap in the North Pacific Ocean, immature Bristol Bay sockeye generally dominated in 1956, 1957, 1959 and 1960, and immature Kamchatkan sockeye dominated in 1958.

6 (a). From the results of tagging experiments it has been shown that the maturing sockeye having originated in rivers tributary to the northeast Pacific Ocean (i.e., from the Chignik River on the south side of the Alaska Peninsula eastward and southward to the Columbia River) occur in the spring and summer mainly east of 160°W and north of 49°N, and that they intermingle extensively in these waters. Some individuals of the Chignik River, Kodiak Island, Cook Inlet and Nass River stocks have been found farther west, to about 176°30′W, south of the Aleutians ; some individuals, especially from the stocks originating from southeastern Alaska southward to the Columbia River, have been found as far south as 46°N.

6 (b). Little information is available on the oceanic distribution of the immature sockeye from stocks of the rivers tributary to the northeast Pacific Ocean. Of six recoveries of tagged fish, four had been released east of 157°W and north of 50°N, one had been released immediately south of the Aleutians at 176°30′W (recovered in southeastern Alaska), and one had been released immediately south of the Aleutians at 177°30′E (recovered in Rivers Inlet, British Columbia).

6 (c). Maturing Bristol Bay sockeye intermingle extensively from late April to mid-June with maturing sockeye from rivers tributary to the northeast Pacific in the waters bounded by approximately 58°N, 145°W in the northeast ; 50°N, 148°W in the southeast ; 50°N, 155°W in the southwest ; and 56°N, 155°W in the northwest. The entire known area of overlap in the distributions of maturing sockeye from these two general areas extends eastward to 142°30′W (at 56°N), southward to 46°N (at 155°W), and westward to 176°30′W (at 49°N–51°30′N).

7 (a). Maturing Kamchatkan sockeye appear to winter mainly in the waters off southeastern Kamchatka and southwest of the Aleutians, as far south as at least 44°N. In the spring and early summer months they move progressively in a northwesterly direction towards Kamchatka. Some fish bound for Kamchatka also approach from more easterly waters along the south side of the Aleutians and probably from the Bering Sea, as well.

7 (b). Immature Kamchatkan sockeye apparently have a similar migratory pattern to that of the maturing sockeye, but their general northwestward movement results in their concentrating in the western Bering Sea and western North Pacific Ocean, north of about 52°N, by August. A general return to the more southerly waters apparently occurs in the fall or winter or both, although some fish may remain in the Bering Sea throughout these seasons. The migration patterns of fish in their first year of sea life are unknown, although it is apparent that at least some Kamchatkan sockeye may migrate eastward as much as 1,000 miles during this first year.

7 (c). Maturing Bristol Bay sockeye apparently winter mainly from the northwestern Gulf of Alaska eastward to southwest of the Aleutians, in a band somewhat south of the Aleutians. It appears likely that the main concentrations occur in the more easterly waters. In the spring they move towards the Bering Sea ; those reaching the Aleutians from the south or east give rise to a marked westerly migration, in late May and in June, immediately south of the Aleutians before entering the Bering Sea through various passes. Eastward migration towards Bristol Bay in the latter half of June apparently is preceded by extensive northward dispersal in the Bering Sea.

7 (d). Immature Bristol Bay sockeye apparently winter mainly south of the maturing fish and follow, in time, their general northward and westward migration. From late June through August there is a pronounced westward movement of these immature fish along the south side of the Aleutians. Some of these fish move into the western and central Bering Sea. In the fall or winter or both, most of these immatures return to their wintering areas somewhat south of the Aleutians and in the Gulf of Alaska. However, some fish, whether or not they will mature in the following summer, may winter in the Bering Sea. The movements of Bristol Bay sockeye during their first year in the sea are not known, but fish which have been at sea for about one year have been found near the western Aleutians, i.e., as much as 1,100 to 1,200 miles west of their rivers of origin.

7 (e). Maturing sockeye of the major stocks from the rivers tributary to the northeast Pacific Ocean, being intermixed in the spring months over large areas of the Gulf of Alaska, migrate in various directions towards their rivers of origin. Some stocks migrate coastward earlier than others.

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REPORT OF THE WORKING GROUP ON RESEARCH PROGRAM

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On the basis of the results of the other Working Groups, the Research Program Working Group assigned priorities with respect to (1) the species capable of the greatest increase in yields and (2) the actions necessary to bring these greater yields into being. The possibilities for greater yields were estimated to be as follows:

Species of tuna	Approximate present yield (metric tons)	Potential additional yield (metric tons)
Skipjack	70,000[1/]	150,000 upward
Yellowfin	100,000[2/]	30,000-50,000
Bigeye	100,000[3/]	Little if any

[1/] Exclusive of western Pacific.

[2/] Exclusive of stocks exploited by eastern Pacific surface fishery.

[3/] Japanese longline.

In view of the apparently much greater potential for increased yields in skipjack tuna than in the other species, much of the discussion of actions necessary to increase the yield is centered on it. Much of what is proposed for skipjack tuna, however, may be equally (and simultaneously) applicable to yellowfin and perhaps bigeye tuna.

The discussions are oriented around Hawaii for five reasons: (1) Hawaii is the site of a midocean fishery capable of expansion; (2) since tuna are present the year around in Hawaiian waters, developmental studies can be carried out here most efficiently from a logistic standpoint; (3) Hawaii is strategically located with respect to the development of presently unfished areas; (4) results achieved in Hawaii can immediately be applied in other areas, as for example, the Trust Territory of the Pacific Islands; (5) the events associated with recruitment and escapement of skipjack tuna in the eastern Pacific Ocean occur in the central Pacific and can most conveniently be studied from Hawaii.

With respect to actions necessary to attain greater yields, there are four questions of approximately equal importance, the answers to which must be sought concurrently. These are:

1) How can the fish be caught?

2) Where are the fish abundant?

3) What are the relationships of the fish in the different areas?

4) What is the magnitude and potential yield of the resources?

In discussing the methods of achieving the answers to each question, it should be emphasized that an attempt has been made to express priorities in descending order of importance.

HOW CAN THE FISH BE CAUGHT?

The relatively low annual catch per boat in the Hawaiian live-bait fishery for skipjack tuna has long been known and attempts have been made to improve the catch, largely by trying to improve some aspect of the live-bait segment of the fishery. It is entirely conceivable, however, that some other aspect of the operation is the ''weak link'' and that improvements in this aspect could increase the yield per boat more readily than improvements in the bait. A systems analysis of the fishery is needed and provisions have been made for such an analysis by the Bureau of Commercial Fisheries and the University of Hawaii.

In addition to whatever this study may reveal, there are obvious possibilities for improving the live-bait aspect of the fishery. These include (1) improved bait handling at capture, (2) improved bait handling aboard ship, (3) culture of bait fish, and (4) introduction of bait fish. Work is in progress or in prospect on (1), (2), and (3) by Bumble Bee Seafoods, the Bureau of Commercial Fisheries, the Hawaii Division of Fish and Game, and the University of Hawaii. The introduction of bait fish is being deferred pending determination of a good bait species.

Forms of gear other than pole and line which would increase the catch of skipjack per unit of bait or which would eliminate the need for bait entirely would have obvious advantages. The Norwegian bluefin tuna purse seine, a relatively lightweight, rapidly operable purse seine, is fished from vessels of the same length as Hawaiian skipjack vessels. Information is being obtained on the characteristics and operation of this seine. It should be tested in Hawaiian waters.

Regardless of the gear used to take the fish, improvements in the present techniques of locating fish schools could also increase the efficiency of the fishery.

Yellowfin tuna are available to the Hawaiian boats, but are generally not taken by them owing to the ''blood-streaking'' of the fish when canned. If this problem could be overcome, this species would be available to the fleet. In addition, any improvements in skipjack tuna fishing methods would probably apply to yellowfin tuna, as well.

Improvements of the kind discussed above, once attained, could probably be applied immediately elsewhere, as, for example, in the Trust Territory island groups, the Marquesas, and the Line Islands. In the intervening, non-insular areas, the tuna (of the sizes smaller than those taken by longline) are believed to be largely subsurface and it is likely that new methods of locating and capturing the fish in these areas will be required.

Relevant to the development of new methods of capturing tunas are studies (1) of their abilities to see, smell, and hear, (2) of their behavior, and (3) of their vertical distribution and degree of schooling. Information on their senses and behavior has been, and is being, obtained under experimental conditions by the Bureau of Commercial Fisheries and information on behavior, vertical distribution, and schooling will be obtained by the same organization through the use of a CTFM sonar to be installed on the Townsend Cromwell in April 1966.

Once information is available on depth distribution, degree of schooling, swimming speeds...it will be possible to make judgments as to which type of gear is most likely to be successful and to proceed with the development and testing of such gear. Experience elsewhere has shown that gear development is demanding of time and effort. If undertaken, it should be pursued on an adequate basis.

Following the development of gear capable of taking tunas in the non-insular areas, it will be necessary to demonstrate the economic feasibility of a fishing operation based on such gear. This is a process which grades from research and development on the one hand to an active, viable fishery on the other. There is perhaps no clear point in this process at which the responsibility of government ends and the responsibility of industry begins. It seems desirable that industry begin to assume some degree of responsibility rather early in the process.

Again, it is likely that gear development for skipjack tuna in non-insular areas will be effective for yellowfin and bigeye tuna.

WHERE ARE THE FISH ABUNDANT?

In seeking areas where tunas are abundant, it is natural to consider first the areas of existing fisheries. In Hawaii, for example, additional yields of skipjack tuna may be expected through the expenditure of additional fishing effort. Similarly, in the eastern Pacific skipjack tuna fishery additional yield may be expected through additional fishing effort. Conversely, the eastern Pacific yellowfin tuna fishery is already being prosecuted at about the level of maximum sustained yield and additional effort would act to reduce the yield. Some information is also available for areas where no fisheries exist, as, for example, from the fishery surveys carried out by the Bureau of Commercial Fisheries in the Marquesas Islands region, where a latent skipjack tuna resource was found. (Although such surveys provide useful information and may lead to the development of fisheries, the most useful and reliable information will result from the actual development and growth of the commercial fishery itself.)

In seeking to extend such areas of known abundance, it may be best, as seems logical in the Hawaiian skipjack tuna fishery, to proceed by expanding the known range of the resource beyond the area presently fished. This will involve proceeding from the insular surface-school situation to the non-insular subsurface-school situation. As already indicated, this will require the use of new methods of locating the fish. Sonar will undoubtedly play a major role in this search and a research submarine (which can provide a better sonar platform than a surface ship) could also prove invaluable.

Beyond the areas of presently known tuna abundance are undoubtedly other areas of abundance. These could be sought out, for example, by laying out an observational grid or pattern and making a sonar survey of tuna abundance over that pattern. If nothing were known about the biology and oceanography of the tropical Pacific, this would be the best way to proceed. Enough is known, however, so that the observational pattern could be oriented around areas which various lines of evidence suggest may be areas of tuna abundance. Concentrations of tuna larvae indicate the presence of concentrations of spawning adults. The association of skipjack tuna with the broad boundary of the California Current Extension as it moves seasonally through the Hawaiian Islands suggests the association of the species with the boundary when it is south of the Hawaiian Islands, or perhaps with similar boundaries elsewhere. Other features of circulation and water conditions which lead to concentrations of tuna should be sought.

Again, when non-insular areas of tuna abundance are found, given appropriate gear, there is the problem of proving the economic feasibility of a fishery based on that area.

WHAT ARE THE RELATIONSHIPS OF THE FISH IN THE DIFFERENT AREAS?

To insure the orderly and rational utilization of a fishery resource, it is necessary to understand its subpopulation (= basic population unit) structure. For example, are the Hawaiian and eastern Pacific skipjack tuna fisheries based upon the same or different subpopulations? If they are based upon the same subpopulation, then what happens in one fishery may, or most likely will, have an effect upon the other. If they are based upon different subpopulations, then what happens in one subpopulation will have no effect upon the other.

It is possible to approach this problem through the study of inherited blood group systems and other genetically controlled blood characteristics. Such studies made by the Bureau of Commercial Fisheries on the Hawaiian skipjack tuna have shown that the Hawaiian fishery is based upon at least two subpopulations. These studies need to be extended in several ways. First, they need to be intensified in Hawaii to provide more information on, among other things, the relative contributions to the fishery of these two subpopulations throughout the year and their possible associations with the different water masses which bathe the islands at different times during the year. Second, they need to be extended to the eastern Pacific to determine whether the subpopulation(s) there and in Hawaii are the same or different. Third, they need to be extended within the eastern Pacific to determine whether the skipjack tuna in the north and in the south are the same or different. Fourth, the skipjack tuna in the intervening areas between the Hawaiian Islands and the Marquesas need to be sampled to test Rothschild's hypothesis. Fifth, comparison needs to be made between the skipjack tuna of Japan and those of the island groups to the south of Japan. (Arrangements are in progress between the Bureau of Commercial Fisheries and the Japan Fishery Agency to institute such studies as part of the international Cooperative Study of the Kuroshio.) Finally, intra-archipelago comparisons are needed.

Continued cooperation between laboratories concerned with these problems is desirable. It is particularly noted that laboratories which can most conveniently obtain the appropriate samples in the eastern Pacific could contribute greatly to the solution of the question of the identity or non-identity of the Hawaiian and eastern Pacific subpopulations by collecting such samples.

As the subpopulations of various fisheries are defined, carefully designed tagging experiments will be necessary to determine rates of exchange, migratory routes.... To answer the questions posed, the design of tagging experiments will have to take into account fish size (''season'' skipjack tuna tagged in Hawaii would not be recovered in the eastern Pacific even if the subpopulation were the same in both places), the location of fisheries (tagging skipjack tuna of a subpopulation which is never fished cannot be expected to produce recoveries)....

Although blood group studies have been made of yellowfin tuna, they are not yet sufficiently advanced to be applied to the problem of subpopulation identification. Continued effort should therefore be applied to these studies so that they may be brought to the point of application. Once this stage is reached there are two problems of pressing importance: (1) comparative subpopulation studies of central Pacific and eastern Pacific yellowfin, and (2) comparative studies within the eastern Pacific of yellowfin tuna from the northern and southern areas.

In this respect it should be noted that it is presently possible to devise a meaningful oceanwide tagging program on yellowfin tuna (as contrasted with the tactics relevant to skipjack tuna). This is so because there is an oceanwide fishery (longline) on large adults, and small yellowfin tuna are easily available, at least in the vicinity of islands. Properly designed, such a program should reveal the broad outlines of the subpopulations and provide information for calculating better estimates of potential yield.

Blood group studies of bigeye tuna are advanced to the point where they could be applied to the problem of subpopulation identification. For the moment, such application appears to be of rather low priority as compared with the skipjack and yellowfin tuna problems, but sampling opportunities might be seized should they become available.

WHAT IS THE MAGNITUDE AND POTENTIAL YIELD OF THE RESOURCES?

To be able to make intelligent decisions about investments and to manage resources wisely, it is necessary to have information about the magnitude of the resources, or at least of the yields they are capable of sustaining. These estimates are difficult to make and it is therefore desirable to use as many different independent methods as possible. Perhaps paradoxically, the ability to make these estimates improves as the fisheries on the resources develop. At any rate, adequately documented fisheries (in terms of catch and effort statistics) provide the basis for the estimates. Existing fisheries, such as those in Hawaii and the eastern Pacific, are well documented and care should be taken to see that this condition continues. Developing fisheries, such as the one in Palau, always should be adequately documented from their inception. Where fisheries have not been completely documented (as may have been true in the early years of the post-World War II Japanese longline fishery), an attempt should be made to reconstitute the records. This work can perhaps best be arranged to meet the needs of particular problems and on a more or less informal basis between laboratories.

Carefully designed tagging experiments are valuable, where there are fisheries and thus recovery facilities, for providing estimates of vital statistics. At present, and for this particular purpose, there are no pressing needs for this kind of information in the Hawaiian skipjack tuna fishery but the framework for a successful experiment does not exist. In the meantime, additional information may be extracted from the data of previous tagging experiments.

Considering yellowfin tuna, the fisheries needed for tag recovery already exist, so that it is possible now to mount meaningful, extensive tagging experiments. These, if properly designed, would resolve the relations among the stocks and provide a better basis for estimating the yield potential.

Other estimates of resource magnitude might be based on surveys of the distribution and abundance of tuna larvae or on surveys of adult tuna by sonar. Both are likely to be expensive to conduct and difficult to interpret. There seems to be no need for these surveys at the moment, except perhaps for particular problems greatly restricted in time and space.

Another independent line of evidence may be derived from calculations of energy flow through the various trophic levels. At present this line of reasoning has so many uncertainties that the results have more interest than value. These uncertainties are not a result of the method, but rather a reflection of our ignorance of the broad details of the paths of biological energy in the sea. Basic studies of energy flow by marine laboratories of universities should help to remove the uncertainties.

Another important area of ignorance concerns the relation of the tunas to the other organisms at the same trophic level, such as the sharks, billfishes.... By selective fishing on only some of the components--the tunas--in this system, some sort of a distorting strain is placed on the system. How important the distortion may be is not known. It is known that striking changes can be wrought in terrestrial situations by such selective pressure. It has been suggested that the decline in abundance of the sardine and the concurrent increase in abundance of the anchovy (off the west coast of North America) is an example of such a dislocation. If it is possible that selective fishing on one or a few components of a trophic level may produce undesirable results, the corollary is that it should also be possible to manipulate the system to produce desirable results. It is possible only to conjecture at this point, but here is an area in which information is needed.

DISCUSSION

Mr. Yoshiro Nakamura asked about the life expectancy of skipjack tuna. Was it no more than 3 years? Dr. Sette said that the exact age attained was unknown, but that he thought it very probable that the harvest will be restricted to the first 3, and possibly up to 5, years of life. ''I'm afraid that that is a very poor answer to your question. I think when you get to fishing on these larger, older stocks, we will have better information on that.''

Mr. John Lanham said, ''I want to ask a question in favor of the fish. Is anybody doing anything to conserve the fish? I imagine sooner or later man will learn how to catch them as fast as he wants to. Is any effort being made to conserve or replace fish in the ocean?'' Chairman Marr replied, ''Yes, we can use conservation in the sense of harvesting the fish at a maximum sustainable yield, which means that you would be harvesting them at a rate that could be continued forever. Many of the kinds of studies that are being made lead to this.''

Asked how with present methods the efficiency of harvesting of surface schools can be improved, Chairman Marr said, ''At the present moment one possibility that occurs to me is that, on the basis of observations made on fish caught at sea and on observations made in our experimental tanks, the good biting schools are those that have not yet located natural feed. There are two periods of biting: one early in the morning, one around noon or late afternoon. The suggestion I would make is that if a school is chummed and doesn't respond immediately, you might assume that is a school that has already fed and you are not going to catch anything from it, and go look for another one.''

In response to a question on how the fishing industry could get additional money to help get into net fishing, Chairman Marr suggested that the speaker investigate the Bureau of Commercial Fisheries loan program.

Another participant asked about the possibilities of export business after the catch had expanded to where it could produce enough to export.

Chairman Marr replied, ''This is an excellent question and one we should have covered before. The very attractive thing, in my mind, about the aku industry is that this is an export product. We export it to the Mainland, primarily, and growth would certainly come in that area.'' As far as fish caught on longlines are concerned, he said, we get into a different problem. ''I think, really, we should have product development before there would be an export market.''

Reprint In Thomas A. Manar (editor), Proceedings, Governor's Conference on Central Pacific Fishery Resources, State of Hawaii, Honolulu, 1966.

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CATCH AND EFFORT STATISTICS FOR THE EASTERN PACIFIC TUNA FISHERY

By

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ABSTRACT

The eastern Pacific tuna fishery extends from southern California to northern Chile and from the coast to about 600 miles offshore. It relies primarily upon yellowfin tuna (Thunnus albacares) and skipjack tuna (Katsuwonus pelamis), but sizeable quantities of albacore (T. alalunga) and bluefin tuna (T. thynnus) are also taken. Bigeye tuna (T. obesus) are caught sporadically. Most of the yellowfin and skipjack tunas are taken either by purse seiners or bait boats, the albacore by bait boats and trollers, the bluefin tuna by purse seiners, and the bigeye tuna by bait boats. Before 1956 about 81 percent of the yellowfin tuna and 90 percent of the skipjack tuna were caught by bait boats, but after 1959 most of the catch was made by purse seiners. This shift was due to the conversion of bait boats to seiners between 1956 and 1959. From 1956 to 1964 the number of bait boats declined from 175 to 35 and the number of seiners increased from 64 to 111. The total catch of all species has increased steadily over the years. Of the total of 400.5 million pounds (181,632 metric tons) of tunas caught in this fishery in 1964, the yellowfin tuna represented 49.4 percent, skipjack tuna 31.2 percent, albacore 12.0 percent, and bluefin tuna 7.4 percent. The catch of bigeye tuna was negligible.

Since 1956 the Japanese longliners have extended their equatorial fishery for yellowfin and bigeye tunas eastward to the vicinity of the Galápagos Islands. By the end of 1962 they had increased their fishing effort to 16 million hooks and 8,000 fishing days per year. In 1962 this fishery produced nearly 15 million pounds (6,803 metric tons) of yellowfin tuna and over 54 million pounds (24,490 metric tons) of bigeye tuna. The yellowfin tuna catch amounted to about 8 percent of the total U.S. yellowfin tuna landings. None of the fish was landed in American ports.

INTRODUCTION

The eastern Pacific in 1964 produced 96.8 percent of the total tuna landed in the United States by vessels of U.S. registry. The fishery generally extends from southern California to northern Chile and from the coast to approximately 600 miles offshore. It primarily relies upon yellowfin (*Thunnus albacares*) and skipjack (*Katsuwonus pelamis*) tunas, but sizeable quantities of albacore (*T. alalunga*) and bluefin tuna (*T. thynnus*) are also taken. A fifth species, the bigeye tuna (*T. obesus*), is caught sporadically in small quantities, incidental to the catches of yellowfin and skipjack tunas (Alverson and Peterson, 1963). In the 10-year period 1953-62 yellowfin tuna accounted for 45.4 percent; skipjack tuna 39.3 percent; albacore 10.2 percent; and bluefin tuna 5.0 percent of the average annual catch (data from Clemens and Craig, 1965; Inter-American Tropical Tuna Commission, 1965; Lyles, 1965a). The average annual dollar value of fish taken over the same 10-year period was $19.8 million for yellowfin tuna, $13.2 million for skipjack tuna, $6.7 million for albacore, and $2.8 million for bluefin tuna (FAO, 1957, 1962, and 1964).

Farther to the west in the area bounded by lat. 10° N. and 15° S., and long. 85° and 130° W., the Japanese began fishing for tunas and billfishes (Istiophoridae) in late 1956. By 1962 they had increased their catches of tunas, particularly bigeye tuna, to sizeable quantities.

YELLOWFIN AND SKIPJACK TUNAS

Method of Capture

The bulk of the yellowfin and skipjack tunas in the U.S. eastern Pacific fishery is caught by vessels of American registry operating mainly from California ports. Most are taken either by purse seiners, which use large nets exclusively, or by bait boats, which fish with pole and line and live bait. Some fish are also caught by trollers incidental to fishing for albacore, but the amounts are negligible when compared with the total landings of the bait boats and purse seiners. In the area farther to the west yellowfin tuna are taken by longline vessels operated by the Japanese.

Fishing Areas

The bulk of the U.S. catch is taken within a few hundred miles of the mainland and around the outlying islands (fig. 1). Within this extensive region the areas which, on the average, consistently yield good catches of yellowfin tuna lie

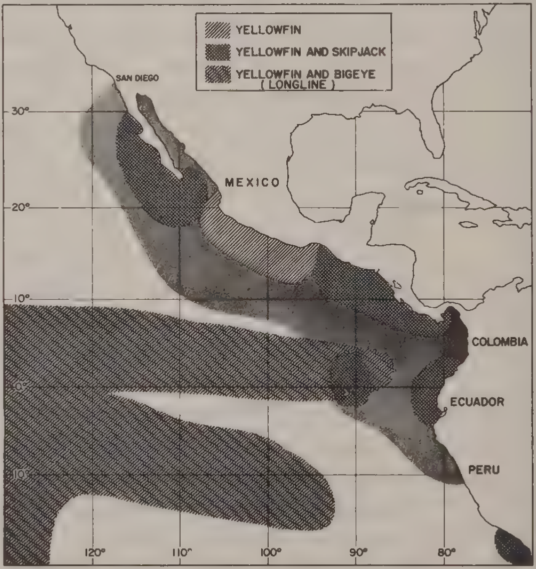

Figure 1.--Principal commercial fishing grounds (lightly shaded area) for skipjack and yellowfin tunas in the eastern Pacific. Darker shadings indicate most productive areas. (Data from Alverson, 1960 and 1963; Suda and Schaefer, 1965.)

off Baja California, Mexico, Central America, Ecuador, and the Revillagigedo Islands. In some years good catches of yellowfin tuna are made off Peru and around the Galápagos Islands by bait boats and off Colombia and Chile by purse seiners (Alverson, 1960 and 1963). The areas which consistently produce good catches of skipjack tuna lie off Baja California, Central America, Colombia, Ecuador, and Chile. In some years good catches are made off Peru and near the Galápagos and Revillagigedo Islands.

The Japanese longline fishery for yellowfin tuna is an eastward extension of their previous fishing area for yellowfin and bigeye tunas in the central Pacific Ocean. If long. 130° W. is selected as the western limit of the eastern Pacific fishery, yellowfin tuna are taken in an extensive area bounded by lat. 10° N. and 15° S. and by long. 85° and 130° W. (fig. 1). The catches are generally small, but the best fishing area appears to be between lat. 3° and 13° S. and long. 105° and 115° W.

Fishing Season

Although yellowfin and skipjack tunas are taken in the same general areas some differences are evident in the catches of the two species: (1) the yellowfin tuna catch is substantial off Mexico, but that of skipjack tuna is relatively poor, (2) skipjack tuna catches show greater seasonal changes than those of yellowfin tuna in the northern part of the fishery, and (3) 60 percent or more of the total catch of yellowfin tuna is taken in the first two quarters of the year, with the peak catch in the second, whereas approximately 60 percent of the catch of skipjack tuna is taken in the second and third quarters, with the peak catch in the third quarter.

Catch records by quarters for 1951-62 (Alverson, 1960 and 1963) show that during January-March the best yellowfin tuna catches are made off Mexico and Central America. Good catches are made off Baja California and the Revillagigedo Islands, and moderate catches off Ecuador. The best catches of skipjack tuna, however, are made off Ecuador, and moderate catches are made off Central America, Chile, and the Galápagos Islands. Skipjack tuna catches are poor at the northern extremity of the area, off Baja California, and near the Revillagigedo Islands.

During April-June catches of yellowfin tuna are again best off Mexico and Central America, and good off Baja California, the Revillagigedo Islands, and Colombia. Catches are moderate off Ecuador. A different situation exists in the skipjack tuna catches: Catches are best off Ecuador, Colombia, and Central America; good in the northern part of the area, off Baja California and the Revillagigedo Islands; and poor off Mexico and at the southern extremity of the fishery off Chile.

During July-September the areas of good catches for yellowfin and skipjack tunas coincide. Catches are best off Baja California, substantial off Central America, and moderate off Ecuador. The catches off Colombia, Mexico, and the Revillagigedo Islands are greatly reduced.

During October-November the areas of best catches differ slightly for the two species. The catches of yellowfin tuna are best off Mexico and moderate off the Revillagigedo Islands and Ecuador. The best catches of skipjack tuna are made off Ecuador and Baja California, and moderate catches are made off Central America.

The offshore longline fishery shows no striking change in the seasonal distribution of yellowfin tuna north of the Equator. The best fishing, however, appears to come in the second quarter. To the south of the Equator there is some evidence of marked seasonal changes in the location of major concentrations. In the first and second quarters a notable concentration of yellowfin tuna develops in the vicinity of lat. 5° S. The area of concentration shifts southward in the third and fourth quarters; in the fourth quarter the best catches are made between lat. 8° and 13° S. (Suda and Schaefer, 1965).

Fishing Effort

As in other fisheries elsewhere, a number of changes have come about in the California-based tuna fishing fleet and in individual vessels over the years, owing to technological advances in gear research and to economic reasons. After the development of synthetic fibers and the Puretic power block, many of the larger boats (over 100-ton capacity) were converted to purse seiners. The greatest change occurred after 1959.

In the several years before the change-over (1956-59), the bait boats numbered between 141 and 175 (table 1) and made up 73 to 78 percent of the combined bait and purse seine fleet. The change-over was so rapid that by 1963 only 30 bait boats were left, which composed 21 percent of the fleet, and of which only 13 were larger than 100 tons.

During the same period the number of purse seiners, which had averaged 53 vessels in 1956-59, increased to a high of 114 by 1961 (an increase from 27 to 72 percent of the fleet), and was 111 (76-78 percent of the fleet) in 1963 and 1964.

As a result of this change in fleet composition, the bait boats, which took an average of nearly 81 percent of the yellowfin tuna catch in 1948-57, took a progressively smaller fraction of the catch in subsequent years; by 1964 the percentage had declined to 5.9 (table 2). The skipjack tuna catch by bait boats

Table 1.--Number of bait boats and purse seiners based in U.S. ports (including Puerto Rico) in 1956-64 (from Schaefer, 1963 and IATTC, 1965)

Type	Size class	Capacity (tons)	1956	1957	1958	1959	1960	1961	1962	1963	1964
Bait boats	1	Under 51	12	11	12	13	10	11	13	13	16
	2	51-100	11	11	8	8	7	4	4	4	5
	3	101-200	43	43	35	31	21	17	12	11	11
	4	201-300	66	60	56	46	11	1	1	2	2
	5	301-400	32	35	36	33	17	11	6	0	1
	6	Over 400	11	10	11	10	3	0	0	0	0
		Total	175	170	158	141	69	44	36	30	35
Purse seiners	1	Under 51	-	-	-	1	-	-	-	-	-
	2	51-100	12	9	8	5	4	3	-	-	-
	3	101-200	50	39	34	39	43	48	33	32	29
	4	201-300	2	2	2	6	23	34	36	33	34
	5	301-400	-	-	-	2	12	22	25	30	28
	6	Over 400	-	-	-	-	-	7	9	16	20
		Total	64	50	44	53	82	114	103	111	111
	Grand total		239	220	202	194	151	158	139	141	146

also declined from an average of 89.5 percent before 1960 to about 12 percent in 1963 and 1964.

Effort in longline fishing is usually expressed as number of hooks. Suda and Schaefer (1965) have summarized the fishing effort in terms of both number of fishing days and number of hooks fished each year in 1956-62 (fig. 2). In the 4 years following the start of the Japanese longline fishery in the eastern Pacific in 1956, the effort remained between 2.9 and 4.7 million hooks; by 1961 and 1962 it had increased to over 11 million hooks.

The increase in effort reflects the development of the fishery. Suda and Schaefer divided the development of this fishery into three periods:

Period I, 1956.--Initially the fishery represented an easterly extension along lat. 6° to 8° N. of the previously exploited yellowfin and bigeye tuna fishery in the central Pacific. Although the fishery began north of the Equator, operations quickly spread southward.

Period II, 1957-60.--After 1956, the fishery north of the Equator spread gradually eastward, but the major concentration of effort developed south of the Equator. The southerly expansion seems to have been encouraged by a good catch of yellowfin tuna in 1957 in the vicinity of the Equator. The average annual number of fishing days during this period was about 1,900, and the number of hooks fished per year was 3.0 to 3.5 million.

Period III, 1961-62.--In 1961 the fishing grounds were extended rapidly eastward and fishing effort increased, particularly in the area north of the Equator. South of the Equator the eastward movement did not extend far east of long. 90° W., owing to a decrease in the catch

Table 2.--Percentage of landings of yellowfin and skipjack tunas taken by California-based bait boats for the years 1948-64 (from Schaefer, 1963 and IATTC, 1965)

Year	Yellowfin	Skipjack
1948	81.9	92.3
1949	86.6	94.1
1950	80.6	89.6
1951	90.8	88.7
1952	82.8	87.2
1953	73.1	90.8
1954	85.9	87.8
1955	77.8	88.8
1956	72.9	95.3
1957	76.5	93.5
1958	66.4	92.5
1959	49.5	87.8
1960	22.9	74.7
1961	12.6	30.0
1962	12.9	14.2
1963	11.0	11.9
1964	5.9	12.2

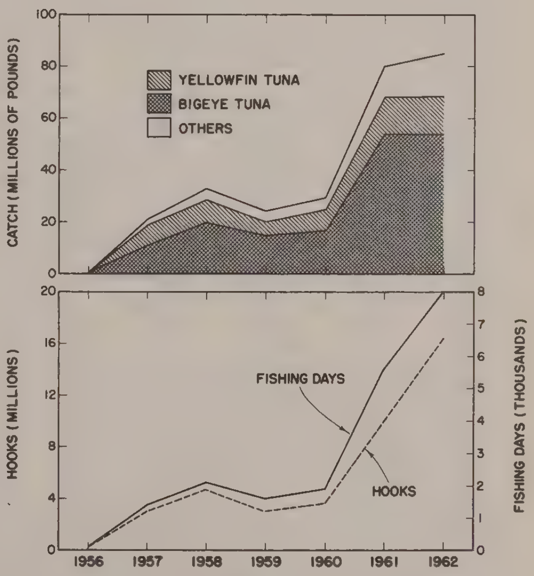

Figure 2.--Estimated annual total fishing effort and catch by the Japanese longline fishery in the eastern Pacific Ocean. (Data from Suda and Schaefer, 1965.)

rate. The number of fishing days in this period is estimated at 5,500 in 1961 and 8,000 in 1962 and the number of hooks at 11 million and 16 million.

Total Landings

Catch records for skipjack tuna date back to 1917, but it was not until 1919 that both yellowfin and skipjack tunas were reported (table 3). The total catch for the two species was 7.2 million pounds; by 1925 it had increased to 27 million pounds. With increasing demand for tuna, the evolution of the modern high-seas tuna fishing fleet, and--beginning in 1926--expansion of the fishery into equatorial regions (Shimada and Schaefer, 1956), the catch increased from 33 million in 1926 to 77 million pounds in 1930 (fig. 3). In 1935 the catch reached 89 million pounds. With the establishment of a cold storage plant in Costa Rica in 1936, the catch of yellowfin and skipjack tunas rose above 100 million pounds and climbed to 172 million pounds by 1940.

The total catch of yellowfin and skipjack tunas decreased during World War II to a low of 80 million pounds in 1943. After the war, as the size of the California fleet increased rapidly, the catch increased correspondingly, and by 1950 the total had reached more than 354 million pounds. In 1951-58 the total

Table 3.--Tuna catch (millions of pounds) in the U.S. eastern Pacific fishery, 1911-64[1]

Year	Yellowfin	Skipjack	Albacore	Bluefin	Total
1911	-	-	0.8	-	0.8
1912	-	-	3.4	-	3.4
1913	-	-	6.6	-	6.6
1914	-	-	18.5	-	18.5
1915	-	-	21.0	-	21.0
1916	-	-	22.9	20.5[2]	43.4
1917	-	0.4	30.6	1.1	32.1
1918	-	3.0	7.3	6.2	16.5
1919	0.3	6.9	13.6	14.9	35.7
1920	1.9	7.9	18.9	10.5	39.2
1921	1.2	1.1	15.3	2.0	19.6
1922	7.3	11.9	13.2	2.8	35.2
1923	10.8	11.5	12.5	3.3	38.1
1924	3.1	3.8	17.7	3.2	27.8
1925	13.2	14.2	22.2	3.8	53.4
1926	12.6	21.0	2.5	6.5	42.6
1927	25.9	33.8	4.6	4.9	69.2
1928	32.2	15.8	0.3	13.7	62.0
1929	37.4	27.0	0.3	7.5	72.2
1930	56.6	20.5	0.3	21.9	99.3
1931	36.6	16.5	<0.1	3.5	56.7
1932	36.9	21.6	0.6	1.1	60.2
1933	51.1	16.7	<0.1	0.6	68.4
1934	60.9	14.8	0.1	18.4	94.2
1935	72.3	17.2	2.4	25.2	117.1
1936	78.3	27.0	1.0	18.9	125.2
1937	91.5	47.1	3.7	12.7	155.0
1938	78.3	22.7	18.9	17.7	137.6
1939	110.4	30.1	19.2	11.8	171.5
1940	114.6	57.6	14.5	20.0	206.7
1941	76.8	25.8	12.0	9.5	124.1
1942	42.0	39.0	23.5	12.8	117.3
1943	50.1	29.4	37.6	10.2	127.3
1944	64.1	31.2	53.2	20.3	168.8
1945	89.2	34.0	40.8	20.6	184.6
1946	129.7	42.5	24.5	22.0	218.7
1947	160.1	53.5	27.7	20.8	262.1
1948	200.3	61.5	51.7	6.5	320.0
1949	192.5	81.0	57.1	4.4	335.0
1950	224.8	129.3	74.3	2.8	431.2
1951	183.7	121.1	34.6	3.9	343.3
1952	192.2	90.8	52.7	4.6	340.3
1953	138.9	133.7	34.7	9.8	317.1
1954	138.6	173.7	27.0	21.0	360.3
1955	140.9	128.0	29.7	13.6	312.2
1956	177.0	150.3	41.3	12.6	381.2
1957	163.0	128.3	46.7	20.3	358.1
1958	149.9	164.9	38.4	30.7	383.9
1959	145.4	177.6	46.4	15.2	414.6
1960	234.2	110.5	40.7	11.9	397.5
1961	239.8	143.1	32.8	20.9	436.6
1962	172.5	161.4	45.9	31.2	411.0
1963	144.3	205.1	60.8	30.4	440.6
1964	197.7	125.2	48.0[3]	29.6[4]	400.5

[1] Sources of data were as follows: Yellowfin and skipjack tunas, 1917-39--Lyles, 1965a; 1940-64--IATTC, 1965. Albacore, 1911-15 and 1962-63--Lyles, 1965a; 1916-61--Clemens and Craig, 1965; and 1964--Lyles, 1965b. Bluefin tuna, 1916-64--Lyles, 1965a and 1965b.

[2] Figure represents combined catches of yellowfin, skipjack, and bluefin tunas.

[3] Preliminary.

[4] Preliminary. Catch of bigeye tuna in Hawaii not included.

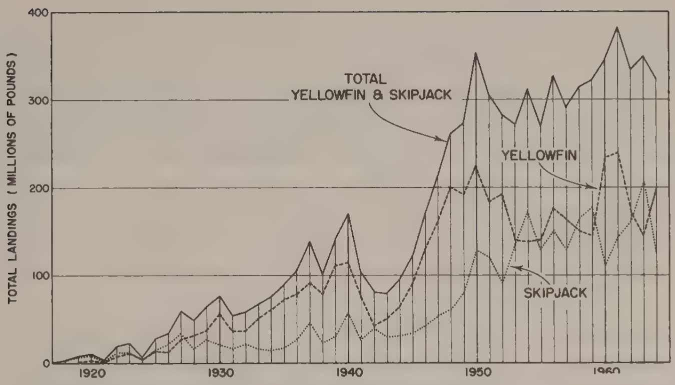

Figure 3.--Total annual landings of yellowfin and skipjack tunas in the U.S. eastern Pacific fishery. (Data from Lyles, 1965a for 1917-39, and IATTC, 1965 for 1940-64.)

annual catch fluctuated between 269 and 327 million pounds (average, 297 million). With the increased conversion of the larger bait boats to purse seiners in 1959, the total catch reached a record 383 million pounds in 1961, and averaged 343 million pounds in 1959-64.

The estimated catch of yellowfin tuna in the Japanese longline fishery is insignificant when compared with the catch made in the U.S. eastern Pacific fishery. In both 1961 and 1962 the longline fishery took 14.7 million pounds of yellowfin tuna (table 4), which represented only 6.1 and 8.5 percent, respectively, of the total U.S. landings.

Abundance

Although the trend for the combined catch of yellowfin and skipjack tunas shows a relatively gradual increase over the years, the catch record by species is completely different. To determine changes in abundance of yellowfin tuna Shimada and Schaefer (1956) and Schaefer (1957a) examined the bait boat catch, relative abundance (expressed by catch per standard day's fishing), and the calculated relative fishing intensity (in thousands of days fishing), for 1934-55 (fig. 4). They found that although the total catch and fishing intensity increased from 1934 to the beginning of World War II, the abundance declined steadily. The decrease in fishing intensity during the war permitted the yellowfin tuna stock to recover to almost prewar levels, but toward the end of the war, as the size of the fishing fleet increased and the total catch rose sharply, the size of the yellowfin tuna stock resumed its downward course. These changes in abundance, which are associated with changes in fishing intensity, proved that fishing affected the size of the stock available for exploitation.

Schaefer (1957b) provided a more exact estimate of the relation of fishing effort to population abundance and catch

Table 4.--Estimated tuna catch (millions of pounds) by the Japanese longline fishery in the eastern Pacific Ocean (data from Suda and Schaefer, 1965)

Year	Yellowfin	Albacore	Bigeye
1956	0.3	-	0.7
1957	7.9	<0.1	11.0
1958	8.8	0.6	19.7
1959	5.1	0.6	15.0
1960	8.3	0.8	16.8
1961	14.7	0.9	53.8
1962	14.7	2.6	54.1

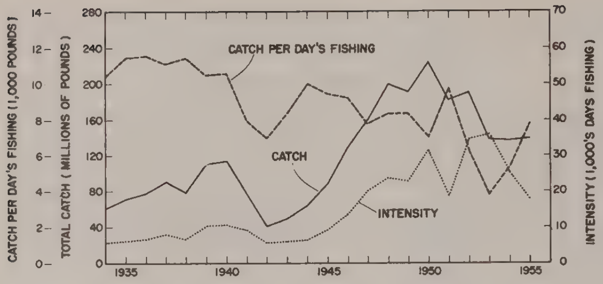

Figure 4.--Total catch, standardized catch per day's fishing, and calculated relative fishing intensity, for yellowfin tuna in the eastern Pacific Ocean. (From Schaefer, 1957a.)

of yellowfin tuna, based on data for 1934-55 (fig. 5). He noted that the estimate, which he called the "line of equilibrium" (shown as the broken line in the figure) was a good fit to the data and that the points for subsequent years, 1956-61, continued to fall reasonably close to the line.

A second "line of equilibrium" calculated from additional data for 1934-61 (shown as a solid line in the figure) was well within the error of estimate of the original line, and thus offered some confirmation of its predictive value. From this new line Schaefer (1963) estimated that the maximum average sustainable catch of yellowfin tuna in the eastern Pacific was about 183 million pounds, at 32,400 units of effort. Subsequent catches for 1962-64 again fell close to the predicted line (IATTC, 1965).

On the basis of these and further studies of the distribution of catch-per-day's fishing by months in 1960-64, IATTC scientists have concluded that the yellowfin tuna population in the eastern Pacific is below that level at which the maximum yield can be sustained.

For skipjack tuna, Shimada and Schaefer (1956) and Schaefer (1961) found that the catch-per-day's fishing fluctuated widely from year to year and did not seem to be associated with changes in fishing intensity (fig. 6). The lack of correlation between the variations in relative abundance of skipjack tuna and the variations in fishing intensity suggested that factors other than the fishery

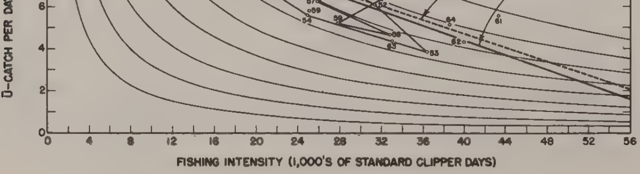

Figure 5.--Interrelations among fishing effort, apparent abundance, and total catch for yellowfin tuna in the eastern Pacific Ocean. (From IATTC, 1965.)

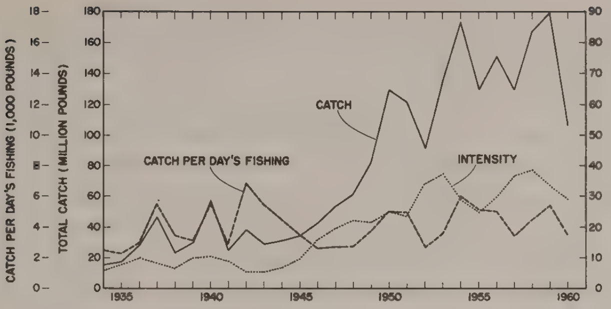

Figure 6.--Total catch, standardized catch per day's fishing, and calculated fishing intensity, for skipjack tuna in the eastern Pacific Ocean, 1934-60. (From Schaefer, 1961.)

have been responsible for the variations in availability of this species. On this basis, Shimada and Schaefer suggested that the skipjack tuna stocks can withstand a much higher level of fishing effort and greater catches before the maximum sustainable yield is reached.

In the longline fishery Suda and Schaefer (1965) showed that there was a general continuous decline in hook rate for yellowfin tuna from the early years through 1962 and that this trend was statistically significant. To examine more analytically the possible relation between fishing effort and apparent abundance, they plotted these variables (fig. 7) and calculated the regression of hook rate on fishing effort.

From the foregoing, it appears that the abundance of yellowfin tuna has decreased as the amount of fishing effort has increased. Suda and Schaefer, therefore, were confident that the abundance of yellowfin tuna available to the longline fishery was actually lower in 1962 than in previous years and that this lower abundance was associated with an increase in fishing effort in the longline fishery. They further suggested that the decrease in abundance may not have been due solely to this increase in effort, but partly to the U.S. fishery farther to the east.

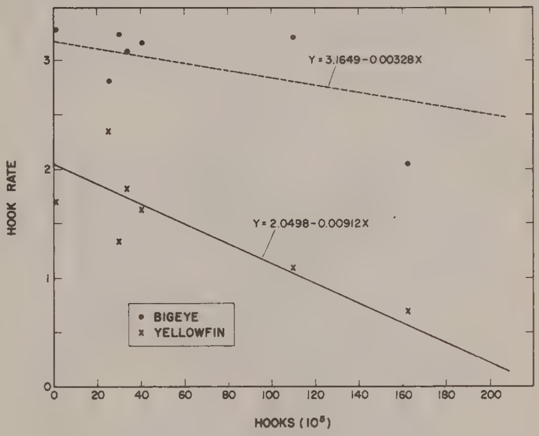

Figure 7.--Relation between annual number of hooks fished and hook rate for yellowfin and bigeye tunas for the eastern equatorial Pacific Ocean, long. 85°-130° W. (From Suda and Schaefer, 1965.)

ALBACORE

Method of Capture

Albacore are taken mainly by pole and line and trolling. The U.S. fishing fleet comprises vessels of various sizes, shapes, and descriptions. The smaller boats, usually under 30 feet long, catch albacore primarily by trolling; larger boats use live bait (Clemens, 1955). Albacore are also taken on longline in the area west of the U.S. fishery.

Fishing Areas

In the U.S. eastern Pacific fishery, albacore have been recorded off Chile, Mexico's mainland, at Clarión Island, and northward along the coasts of Baja California, California, Oregon, Washington, British Columbia, and the Gulf of Alaska (Clemens, 1961a). The most productive fishing grounds are between central Baja California and the Columbia River (fig. 8). Farther to the south, the area of largest catches is off central Chile (de Buen, 1958) and is restricted to within 15 miles of the coast (Manning, 1957).

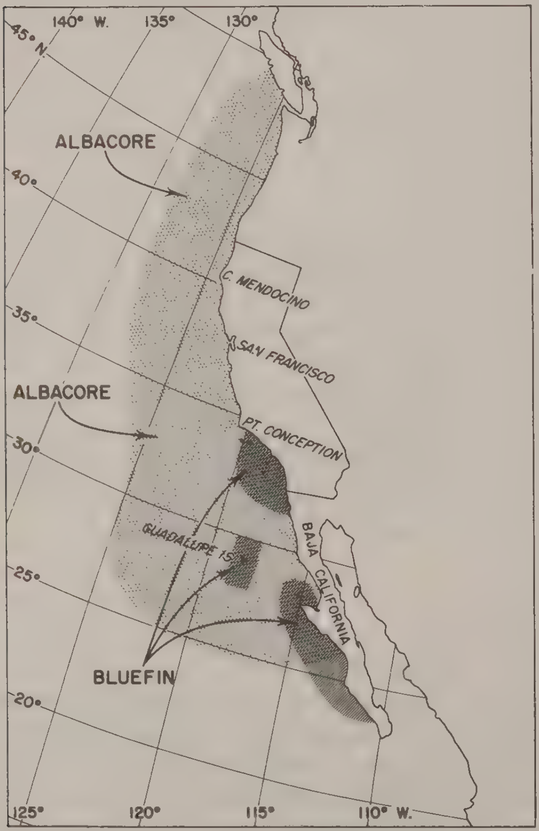

Figure 8.--Principal eastern Pacific commercial fishing grounds for albacore and bluefin tuna. (Data from Clemens, 1961a, and Bell, 1963.)

In the Japanese longline fishery, the area of largest catches extends from lat. 9° to 20° S. and long. 120° to 130° W. Inasmuch as the annual catches of this fishery are small compared with those of the U.S. eastern Pacific fishery (tables 3 and 4), they are not included in the following discussion.

Fishing Season

The eastern Pacific albacore fishery is highly seasonal--limited largely to summer and fall. Typically, the fishery starts in June, develops rapidly in July, maintains a high level in August and September, drops off rapidly in October and November, and ends in December (fig. 9), but in exceptional years fish are caught from May through January (Clemens, 1955).

Geographically, fishing begins off the northern half of Baja California and expands northward as the season progresses, so that by the end of July albacore are taken as far north as Point Conception (Clemens, 1955). By the end of August the fishery extends to the San Francisco-Monterey area, but the catch north of Point Conception is generally small. By September albacore are taken north of San Francisco and the southern areas become less productive. By November the majority of the fish are taken north of Point Conception.

Total Landings

Albacore contributed the major portion of the eastern Pacific tuna catch before 1926 (table 3 and fig. 10). In 1926 the catch dropped drastically and remained poor (between 0.1 and 4.6 million pounds) until 1937. It increased after 1937, and in 1944, near the end of World War II, was about 53 million pounds. Between 1945 and 1963 the annual landings fluctuated widely, from 24.5 to 74.3 million pounds, and averaged 42.5 million pounds.

Studies of the migration of albacore within the fishing grounds in 1951-57 (Clemens, 1961a) showed that distance from shore of the major part of the albacore run varied considerably within and between seasons, and that the present sport fishing fleet, which is generally equipped for 1-day trips and operates within a few miles of port, experiences poor fishing when the albacore run is well offshore. From this Clemens inferred that major increases in distance from shore of the albacore migration had caused the failure of the commercial fishery in 1926-37, because the commercial fleet had been confined before and during this period to the inshore areas that are now fished by the sport fishing fleet. Repetition of past failures in the albacore fishery is unlikely because the commercial fleet now ranges as far as 300 to 400 miles offshore and is affected less by shifts in the migration routes.

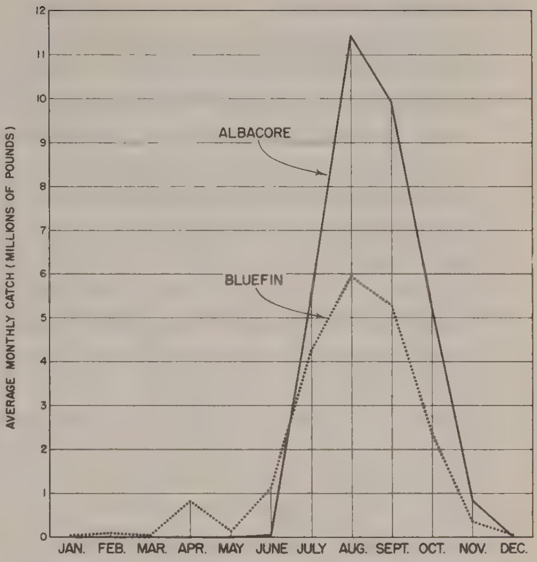

Figure 9.--Average monthly catch of albacore and bluefin tuna in California in 1959-63. (Data from California Department of Fish and Game, 1960-65.)

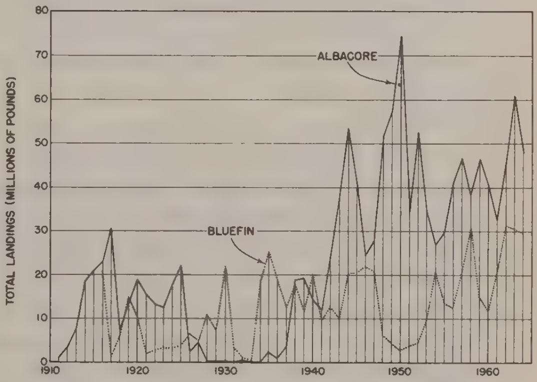

Figure 10.--Total annual landings of albacore and bluefin tuna taken in the eastern Pacific by U.S. vessels. (Albacore data for 1916-61 from Clemens and Craig, 1965; and for 1911-15 and 1962-64 from Lyles, 1965a and 1965b. Bluefin tuna data from Lyles, 1965a and 1965b.)

BLUEFIN TUNA

The bluefin tuna, like the albacore, is a temperate species that enters the fishing area during certain seasons. The bulk of the catch consists of small fish (weighing from 10 to 40 pounds), but runs of larger fish (100 pounds or more), particularly in the sporadic winter catches, are not uncommon. Fish in the commercial catch do not, however, attain the large size of bluefin tuna in the Atlantic (Clemens, 1961b).

Method of Capture

Bluefin tuna, never successfully taken by bait boats, are caught mainly by large purse seiners. It is not an exclusive fishery, however, since boats engaged in other fisheries turn to bluefin tuna whenever they appear. Such boats include seiners between 40 and 90 feet long, some of which fish chiefly for sardines and mackerels. The larger boats, over 100 feet long, which usually fish for skipjack and yellowfin tunas in tropical waters, will either take bluefin tuna to fill out a load of yellowfin or skipjack tuna on the way to port, or fish exclusively for bluefin tuna during the season to take advantage of the short distance to port (Bell, 1963).

The number of large seiners has decreased steadily during the past 10 years and at present the fleet is only about half as large as it was in 1950, despite the conversion of large tuna clippers to purse seiners during 1958 and 1959 (Clemens, 1961b). The number of small vessels landing bluefin tuna fluctuates markedly from year to year, depending on general marketing conditions.

Fishing Areas

In the eastern Pacific, bluefin tuna are taken off Chile, Baja California, and southern California. In the northeastern Pacific, records of capture extend the range from Kodiak, Alaska (Radovich, 1961), to Mexico (Berdegué, 1956), but bluefin tuna are found in commercial quantities only in local areas off southern California and Baja California (fig. 8). The fishery seldom extends more than 150 miles offshore and is confined in all areas to waters about banks and islands or along the coast (Bell, 1963). In the southeastern Pacific, bluefin tuna are found off Chile, as far south as Juan Fernández Islands (Rosa, 1950) at approximately lat. 33° S.; the catch is insignificant, however, compared with that of the fleet based in California.

Fishing Season

The bluefin tuna fishery, like that of the albacore, occurs mainly during the summer. In an average year the season extends from June to September, and the heaviest fishing is in July and August (Godsil, 1949). Bluefin tuna have been taken as early as January and February in some years, but in 1959-63, the beginning of the season varied between April and June and the catch reached its peak in August (fig. 9). Good catches were made from July through October. Thus the fishing season for this species fluctuates more than that for albacore.

Early in the season catches are made near Guadalupe Island and off southern Baja California, and in May or June bluefin tuna begin to appear off southern California. Most observations of bluefin tuna north of Point Conception have been in late summer and fall, suggesting a possible northward movement with the advance of summer, similar to that of the albacore, possibly an inshore flanking movement of the fish along the coast (Godsil, 1949).

Total Landings

Catch records for bluefin tuna date back to 1917 (table 3), when slightly more than 1 million pounds were landed. The catch increased to nearly 15 million pounds by 1919 and except for three major periods of poor catches--1921-27, 1931-33, and 1948-52, when the average annual landings dropped to 4.4, 1.7, and 4.3 million pounds, respectively--the average annual landings through 1963 have not varied appreciably (fig. 10). The average annual landings during the intervening periods of good catches--1928-30, 1934-47, and 1953-63--were 12.3, 17.2, and 19.8 million pounds.

Unlike the landings of skipjack tuna, yellowfin tuna, and albacore, which increased rapidly in the years following World War II, the catch of bluefin tuna remained relatively steady with only minor fluctuations. Before 1946 the bluefin tuna catch exceeded 10 percent of the total tuna catch in 17 of 30 years, but it has not done so since then.

BIGEYE TUNA

In the U.S. eastern Pacific fishery only insignificant quantities of bigeye tuna are taken sporadically off Baja California, off northern South America, and around the Galápagos Islands by the U.S. live-bait fishery. Estimates of the landings extracted from vessel logbook records (Alverson and Peterson, 1963) show that the annual catch has never exceeded 300 metric tons or 0.7 million pounds. Consequently, only the catches by the Japanese longline fishery are discussed here.

Fishing Areas

The Japanese longline fishery for bigeye tuna in the eastern Pacific extends over the same area as that for yellowfin tuna (fig. 1). The bigeye tuna is the dominant species throughout most of the fishing area. An interesting feature of the fishery for bigeye tuna in the vicinity of the Equator is the zone of low hook rates west of long. 115° W., and high hook rates some 5° north and south of the Equator. The low catch rates east of about long. 90° W. indicate that the abundance of tuna drops off in this region (Suda and Schaefer, 1965).

Fishing Season

In the southern zone between long. 100° and 130° W. (fig. 1) the hook rate is highest in the first quarter of the year and lowest in the third quarter; east of long. 100° W. the maximum hook rate is in the third or fourth quarter.

In the area north of the Equator and west of lat. 115° W. catches are highest in the first quarter. In the area between lat. 100° and 115° W. no fishing was done in the first quarter of the years covered; however, fishing was pursued in the second and third quarters, and the catch rates were slightly higher in the third. In the fourth quarter the catch rate dropped slightly, but relatively little effort was expended. East of lat. 100° W., catches seem to change little from quarter to quarter (Suda and Schaefer, 1965).

Fishing Effort

Since yellowfin and bigeye tunas are taken on the longline, the discussion of fishing effort for yellowfin tuna (p. 134) applies equally to bigeye tuna.

Total Landings

As may be seen in figure 2 and table 4, the increase in fishing effort in recent years has been accompanied by a sizeable increase in total catch. The total catch of bigeye tuna increased from 0.7 million pounds in 1956 to an average of 15.6 million pounds in 1957-60 and 53.9 million pounds in 1961-62. The catch of bigeye tuna by the U.S. eastern Pacific fishery in 1961 and 1962 was larger than the albacore catch.

Abundance

Suda and Schaefer (1965) reported that the hook rate of bigeye tuna was nearly stable through 1960, fluctuating about an average value of 3.1 fish per 100 hooks (standard error, 0.184), and that a decline was evident beginning in late 1961 or early 1962. Although this decline in hook rate appeared both in the data for the total area and in individual major fishing areas, they found it impossible to state conclusively that the decline represented real change in the abundance of the species. Considering the large increase in fishing effort in 1961 and 1962, however, and the decline in abundance of yellowfin tuna (discussed previously), they pointed to the possibility that the fishery might be decreasing the stocks of bigeye tuna. When fishing effort and apparent abundance of bigeye tuna were plotted by quarters and by years, however, they found (for both the quarterly and yearly plots) that the regression lines for bigeye tuna did not differ significantly from 0.

ACKNOWLEDGMENTS

Witold L. Klawe and Harold B. Clemens reviewed the manuscript critically and made many helpful suggestions.

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DISTRIBUTION AND ABUNDANCE OF TUNA LARVAE IN THE PACIFIC OCEAN

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ABSTRACT

In the western and central Pacific Ocean, larvae of skipjack tuna (Katsuwonus pelamis) and yellowfin tuna (Thunnus albacares) have been found in the same areas, but in the eastern Pacific larval yellowfin tuna are distributed over a greater area than larval skipjack tuna. Larvae of bigeye tuna (T. obesus) were found chiefly near the Philippine Islands and Formosa in the western Pacific Ocean and near the Hawaiian, Line, and Tuamotu Islands in the central Pacific. Larvae of bluefin tuna (T. thynnus) were restricted to the western Pacific Ocean. Studies of gonads indicated that albacore (T. alalunga) spawn in two zones, one in the western Pacific Ocean north of lat. 10° N., the other in the central Pacific Ocean south of the Equator. In higher latitudes, both skipjack and yellowfin tunas spawn only in summer, but in the equatorial region they spawn throughout the year. Skipjack tuna larvae were far less abundant in the eastern Pacific than in the central Pacific. Yellowfin tuna larvae decreased in abundance from west to east, but less pronouncedly.

INTRODUCTION

Until 1950 very little information existed on the occurrence of larval tunas in the Pacific. Since then the Bureau of Commercial Fisheries (BCF), Honolulu, the Inter-American Tropical Tuna Commission (IATTC), and the Nankai Regional Fisheries Research Laboratory (NRFRL) of the Japan Fishery Agency have collected much material on the identity, distribution, and occurrence of tuna larvae in the Pacific Ocean. The BCF collected more than 3,000 plankton samples (all types of tows) from 1950 to 1964 in the central Pacific Ocean, the IATTC collected more than 800 samples in the eastern Pacific Ocean from 1952 to 1959, and the NRFRL collected approximately 2,300 samples in the western Pacific Ocean from 1949 to 1960 and more than 350 samples in the central and eastern Pacific Ocean during 1962 and 1963 (fig. 1). In addition, plankton samples have been taken in the Pacific Ocean by research vessels such as the Dana (the Carlsberg Foundation's Oceanographical Expedition Round the World 1928-30) and the Vityaz (Institute of Oceanology

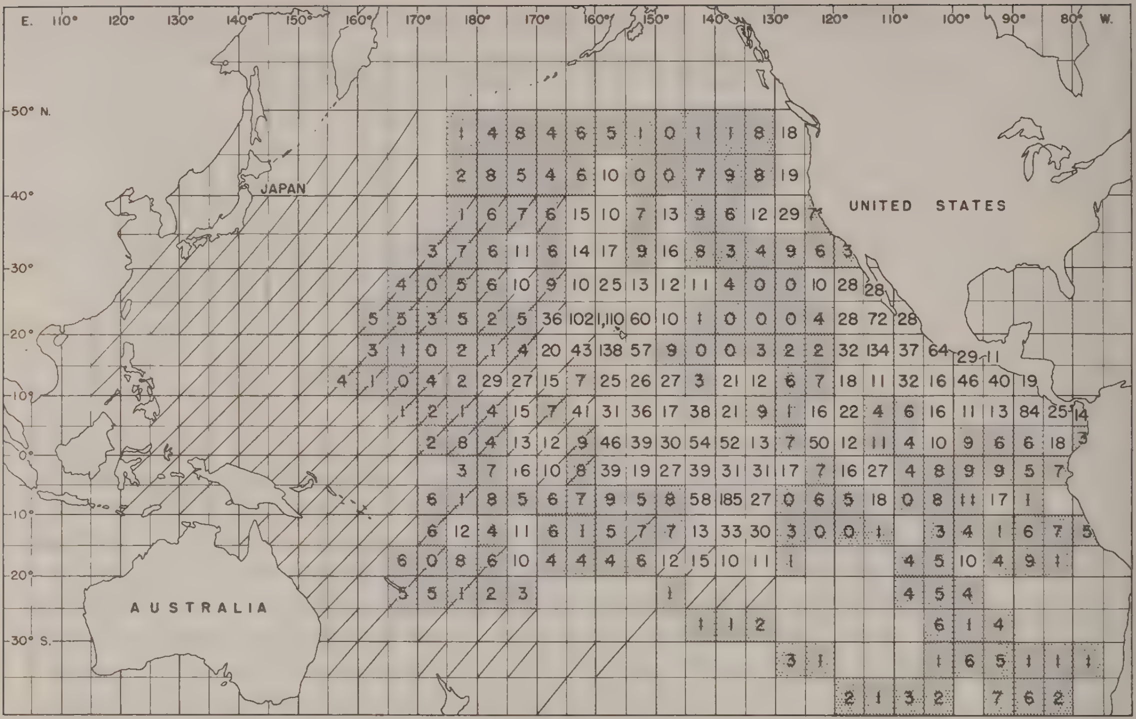
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Figure 1.--Totals of all types of plankton tows taken by the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, 1950-64; the Inter-American Tropical Tuna Commission, 1952-59; the Nankai Regional Fisheries Research Laboratory, 1949-60 (slashed rectangles; numbers not available); R/V _Shoyo Maru_ (Japan Fishery Agency), 1962-63; R/V _Vityaz_ (Institute of Oceanology of the U.S.S.R. Academy of Sciences), 1957-58. (Shaded areas represent less than 10 tows per 5° rectangle.)

of the U.S.S.R. Academy of Sciences). In the eastern Pacific Ocean, the California Cooperative Oceanic Fisheries Investigations (CalCOFI) began large-scale monthly survey cruises in 1949 in an area approximately 400 miles wide and 1,320 miles long off Oregon, California, and Baja California (Ahlstrom, 1954). Over the 10-year period 1951 through 1960 CalCOFI collected about 15,800 plankton samples (numbers not included in fig. 1).

Great strides have been made in identifying the larvae of tuna on the basis of morphology and body pigmentation. Although some problems remain in the identification of several species, with existing information it is possible to examine the occurrence and distribution of most species individually (figs. 2-4).[1]

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[1] The data for figures 2 to 4 were obtained from Wade (1951), Matsumoto (1958), Strasburg (1960), Sun (1960), Yabe and Ueyanagi (1962), Klawe (1963), Nakamura and Matsumoto (in press), and from unpublished material filed at BCF Biological Laboratory, Honolulu.

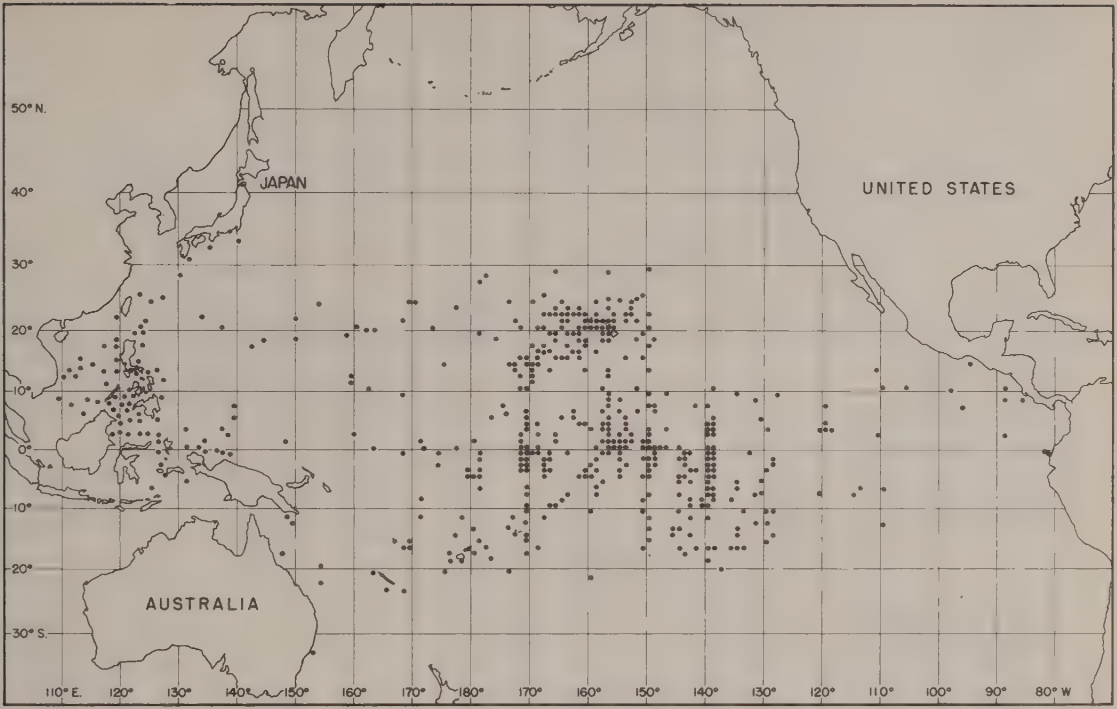


Figure 2.--Locations of capture of skipjack tuna larvae, 1949-64. Larva at lat. 2° N., long. 88° W. is from effort not shown in figure 1. Sources of data listed in text, footnote 1.

GEOGRAPHIC DISTRIBUTION

Tunas are extremely mobile, and individuals of the sizes usually taken by the commercial fisheries occupy a tremendous geographic range. Albacore (Thunnus alalunga) have been caught as far north as lat. 45° N., and fish tagged off the American west coast have been recovered in Japanese waters (Otsu and Uchida, 1963). Bigeye tuna (T. obesus) have been caught from lat. 43° N. to 31° S. and yellowfin tuna (T. albacares) have been caught from lat. 38° N. to 31° S. (Nankai, 1959).

Although adults are caught over a very wide range, the spawning areas as determined by larval distribution, are restricted to tropical and subtropical waters. In the eastern Pacific the north-south range of larval tunas is compressed somewhat by cold water moving toward the Equator from the north and south, whereas in the western Pacific the north-south range is greatly expanded by warm equatorial water moving away from the Equator.

Skipjack Tuna

The distribution of skipjack tuna larvae (fig. 2) differs greatly in the eastern and central Pacific. Larvae are taken in relatively high numbers in the central Pacific with 1-m. plankton nets, but few are caught with such nets in the eastern Pacific. In 8 years of sampling

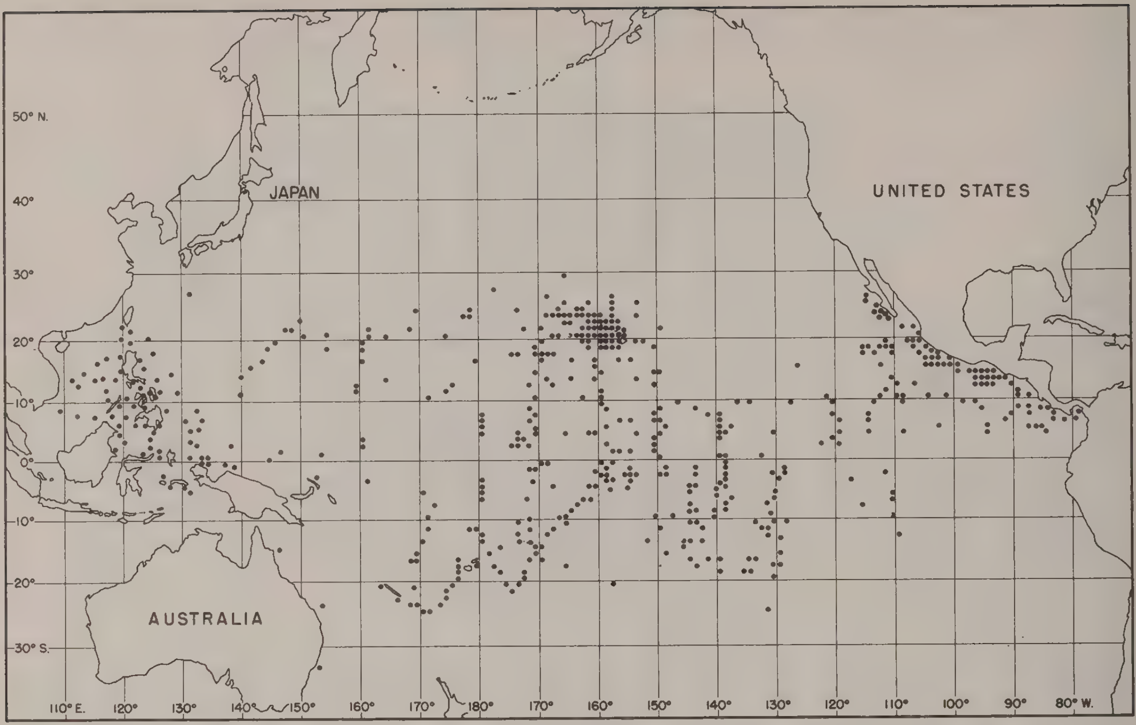
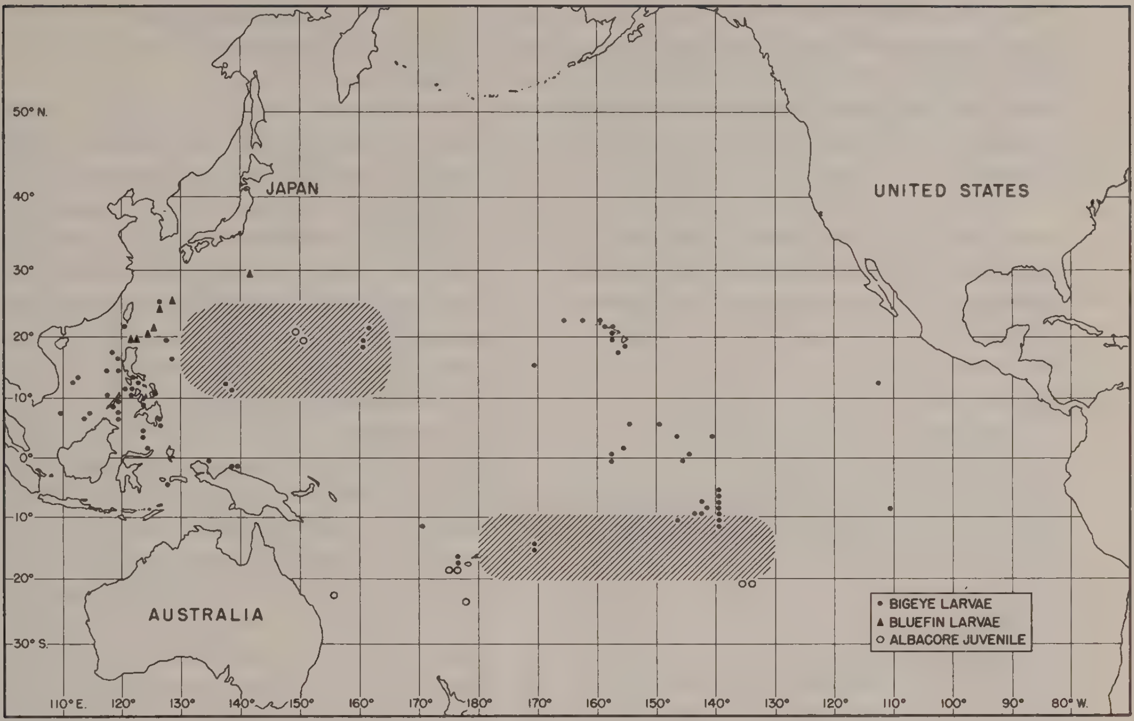


Figure 3.--Locations of capture of yellowfin tuna larvae, 1949-64. Sources of data listed in text, footnote 1. (Larvae taken off Baja California on CalCOFI survey cruises are included.)

in the eastern Pacific, Klawe (1963) found only 20 larvae of skipjack tuna from six localities. He thus concluded that skipjack tuna spawn little in this area. This conclusion was foreshadowed by studies of gonad development (Schaefer and Orange, 1956; and Orange, 1961).

In the central Pacific between long. 130° W. and 180°, skipjack tuna larvae have been taken as far north as lat. 30° N. in the area north of the Hawaiian Islands and as far south as lat. 20° S. near the Tonga Islands. The absence of skipjack tuna larvae in plankton tows north of lat. 30° N. indicates that the 30th parallel may be the true northern limit of spawning in the Hawaiian Islands region. Because few plankton tows have been made south of lat. 20° S. the southern limit of spawning cannot be determined (fig. 1).

In the western Pacific larvae have been taken from as far north as lat. 33°49' N. (Yabe and Ueyanagi, 1962) off the coast of Japan and as far south as lat. 32° S. off the east coast of Australia. The relatively few scattered points showing capture sites of larvae in the area between long. 130° E. and 180° may not represent the true distribution. The Japanese are known to have made hundreds of plankton tows in this area, but to date the results of only a few cruises have been published.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100°
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80° W.
JAPAN
UNITED STATES
AUSTRALIA
• BIGEYE LARVAE
▲ BLUEFIN LARVAE
○ ALBACORE JUVENILE

Figure 4.--Locations of capture of bigeye and bluefin tuna larvae and albacore juveniles, 1949-64. Hatched areas denote probable albacore spawning areas as judged from gonad studies (Ueyanagi, 1957; Otsu and Hansen, 1962).

Yellowfin Tuna

The distribution of localities of capture of yellowfin tuna larvae (fig. 3) in the equatorial Pacific Ocean resembles that for skipjack tuna larvae. Differences are noted, however, in the northward extension of distribution at both the eastern and western extremities. In the eastern Pacific, larvae of yellowfin tuna have been taken in greater numbers, in more collections, and farther to the north than larvae of skipjack tuna. The northernmost record for yellowfin tuna larvae is at lat. 25°49' N. (E. H. Ahlstrom, personal communication) compared with lat. 14°41' N. for skipjack tuna larvae (Klawe, 1963). In the western Pacific, larvae of yellowfin tuna have not been taken as far north as those of skipjack tuna. The northernmost record for yellowfin tuna is at approximately lat. 27° N., compared with lat. 33°45' N. for skipjack tuna.

Bigeye Tuna

Larvae of bigeye tuna have been collected in a much more restricted geographical range, less regularly, and in smaller numbers than larvae of yellowfin or skipjack tuna (fig. 4). Bigeye tuna larvae have generally been taken near land masses, but a few catches have been made in localities far removed from land (long. 110° W., 140° W., and 145° W.).

In the eastern Pacific larvae of bigeye tuna have been taken only near Clipperton Island. The absence of larvae in the coastal waters of the eastern Pacific suggests that spawning may not occur there.

In the western Pacific the northernmost locality at which bigeye tuna larvae have been taken is lat. 25° N., between the islands of Okinawa and Formosa.

Bluefin Tuna

Larvae of bluefin tuna have been taken only in the western Pacific between the Philippine Islands and Japan (fig. 4). All captures have been made north of lat. 19° N.

Albacore

The distribution of albacore larvae is not included in this report because there are still some unsolved problems regarding their identification. Localities of capture of the juveniles (fig. 4), however, show the general areas of the nursery grounds. Two studies on albacore gonads (Ueyanagi, 1957; and Otsu and Hansen, 1962) gave the probable spawning areas for albacore in the Pacific. Development of gonads was advanced in adult albacore taken from two areas (fig. 4), one north of the Equator (lat. 10° to 25° N.; long. 130° to 165° E.), and the other south of the Equator (lat. 10° to 20° S.; long. 130° W. to 180°). Gonadal development was advanced also in albacore taken in the Hawaiian Islands (Otsu and Uchida, 1959). Regarding the southern area, Otsu and Hansen stated that sampling was inadequate between the Equator and lat. 10° S. and that the area shown might extend farther north.

SPAWNING SEASON

Skipjack Tuna

In higher latitudes, skipjack tuna spawn mainly from late spring to early fall. In the equatorial region spawning generally occurs the year round.

In the western Pacific north of lat. 10° N. skipjack tuna larvae are caught mainly from April through July. South of lat. 10° S., larvae are taken mainly from October through February (Yabe and Ueyanagi, 1962).

Spawning of skipjack tuna is also seasonal in the Hawaiian Islands (fig. 5). Data taken at a station 90 miles southwest of Barbers Point, Oahu, occupied once each month from July 1957 through December 1958 (the International Geophysical Year station) indicate that spawning of skipjack tuna began off Oahu in March, reached a peak in July, and then declined sharply by September. No larvae were taken between November

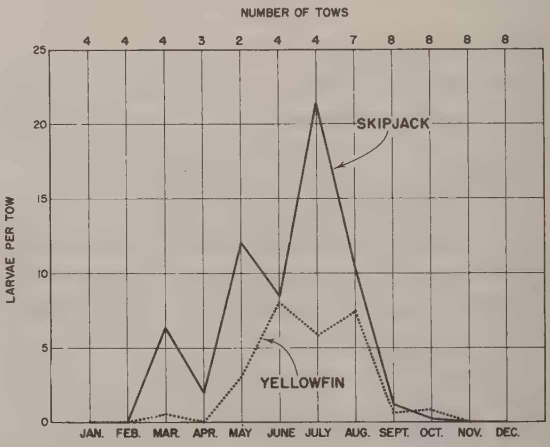

Figure 5.--Average catch of larvae of skipjack and yellowfin tunas by months at the International Geophysical Year station off Barbers Point, Oahu, July 1957-December 1958 (60-m. oblique tow).

and February. Data from plankton catches during other cruises in Hawaiian waters show that skipjack larvae have been caught occasionally in February and October.

Skipjack tuna spawned in each month of the year in equatorial waters south of the Hawaiian Islands (fig. 6), but spawning was heaviest between April and July.

Too few larvae have been taken in the eastern Pacific to present a clear picture of the spawning season. The three captures near Clipperton Island (fig. 2) and the one in the Gulf of Tehuantepec (lat. 14°41' N.; long. 94°56' W.) were made in May, and the two larvae captured along the 88th meridian north of Cocos Island were taken in February.

Yellowfin Tuna

The spawning season of yellowfin tuna is similar to that of skipjack tuna. In the western Pacific, larvae are taken mainly during May and June north of lat. 10° N. and during the entire year in the equatorial region (Yabe and Ueyanagi, 1962).

Spawning of yellowfin tuna is distinctly seasonal in the Hawaiian Islands region (fig. 5). Spawning begins in March or April, reaches a peak from June through August, and drops off sharply in September. No larvae are taken from November through March.

In equatorial waters south of the Hawaiian Islands yellowfin tuna larvae have been taken in all months of the year (fig. 6), but in contrast to skipjack tuna, the yellowfin tuna have displayed no pronounced seasonal peak of spawning. Information from the Marquesas Islands region indicates that peak spawning there occurs during the southern summer (Nakamura and Matsumoto, in press).

Spawning of yellowfin tuna in the eastern Pacific has been discussed in detail by Klawe (1963). The spawning area is divided among three general regions. In the most southerly region, off the coast of Central America between Tehuantepec and Point Mariato (lat. 7°12' N., long. 80°53' W.), spawning is most intensive from January through April, but occurs in all months except August and October. In the outlying Cocos Island area, plankton collections have been few, but larvae were taken in May. Gonad studies by Orange (1961) showed that yellowfin tuna spawn from November to April, with a peak in March.

In the middle region, off the coast of central and southern Mexico, yellowfin tuna larvae were taken primarily during the spring and summer, but some were taken in the fall and winter. Studies of gonads of fish from the outlying Revillagigedo Islands (Schaefer and Orange,

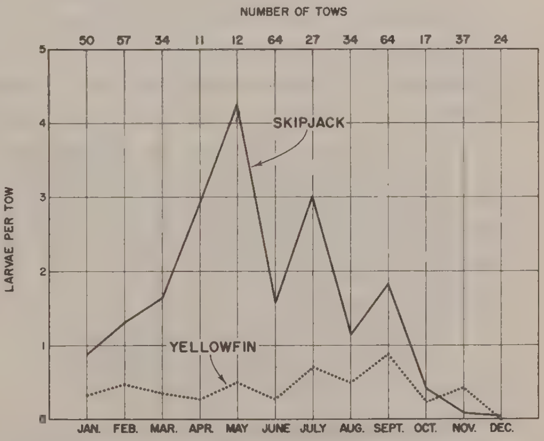

Figure 6.--Average catch of larvae of skipjack and yellowfin tunas by months in equatorial area (lat. 10° N. to 10° S.; long. 130° W. to 180°). (Data collected intermittently over a number of years with 200-m. oblique tows.)

1956; Orange, 1961) indicate that the spawning season near the islands extends from May through September and has a peak in August, but even so only small numbers of larvae were collected in midsummer.

In the most northerly region, off the coast of southern Baja California, spawning of yellowfin tuna is light and usually takes place in early fall.

Bluefin Tuna

Larvae of bluefin tuna in the Pacific have been reported only from the area between Japan and the Philippine Islands (Yabe and Ueyanagi, 1962). These larvae were taken during May and June. Evidently spawning occurs in summer, but neither the length of the season nor the peak spawning period can be established.

Albacore

The spawning season for albacore can only be estimated from gonad studies until identification of larvae of this species is clarified. In the probable spawning area north of the Equator, Ueyanagi (1957) suggested that spawning takes place during the northern summer, with the peak in June and July. In the area delineated by Otsu and Hansen (1962) south of the Equator, the spawning season appears to fall in the southern summer.

RELATIVE ABUNDANCE

Relative abundance of skipjack tuna larvae cannot be compared for the entire Pacific because sampling gear and techniques have not been uniform. In the western Pacific the Japanese sampled with either a 1.4- or 2-m. net towed horizontally for 15 minutes at the surface without a flowmeter. The Philippine Fishery Program used a 1-m. net towed horizontally at the surface for 30 minutes with no flowmeter. The BCF, Honolulu, used a 1-m. net with a flowmeter and employed numerous types of tows over the years. The IATTC used a 1-m. net with a flowmeter and made horizontal tows at the surface and oblique tows to depths of 140 and 300 m. for 30 minutes.

Because of these differences, the comparison below of relative abundance of larvae is restricted to samples collected by the BCF. The most comprehensive sampling both in time and space was with the 200-m. oblique tow. This type of tow yields very small catches, about one-sixth those of the 60-m. oblique or surface tow made at night; some comparisons can be made, nevertheless.

Matsumoto (1958) found a high density of skipjack tuna larvae in the equatorial region and a reduction in average catches northward from the Equator. The area to the south and southeast of Hawaii, between lat. 10° and 15° N., consistently produced small catches of larvae, but in the Hawaiian area the density of larvae was high during the summer (unpublished data; BCF, Honolulu).

Density of skipjack tuna larvae during the peak summer months differed little between the Hawaiian area (lat. 15° to 25° N. and long. 150° to 160° W.) with 2.66 larvae per tow and the equatorial area (lat. 10° N. to 10° S. and long. 130° W. to 180°) with 3.00 larvae per tow.

The density of yellowfin tuna larvae for the same two areas was much different. The catch per tow of 0.66 larva in the Hawaiian area in summer slightly exceeded the catch of 0.50 larva per tow in the equatorial area; however, no yellowfin tuna larvae were taken near

Hawaii from November through February, whereas the density of larvae in the equatorial region remained little changed. On an annual basis, therefore, the equatorial region could have the more yellowfin tuna larvae.

Spawning of skipjack tuna (fig. 2) apparently diminished eastward from the central Pacific along the Equator. Between long. 180° and 105° W. and lat. 10° N. and 10° S., the relative abundance of skipjack tuna larvae generally declined from west to east (fig. 7), but marked concentrations were found at long. 179°-170° W., 154°-150° W., and 144°-135° W. There are no islands in the area between these peaks. The low catches of larvae east of long. 130° W. support Rothschild's (1965) interpretation that the skipjack tuna fished commercially in the eastern Pacific fishery return to the equatorial waters of the central Pacific to spawn.

The westward increase in density is also noteworthy. If this trend continues westward, it is possible that a sizeable portion of the skipjack tuna resources in the Pacific could be west of 180°.
of the 180th meridian.

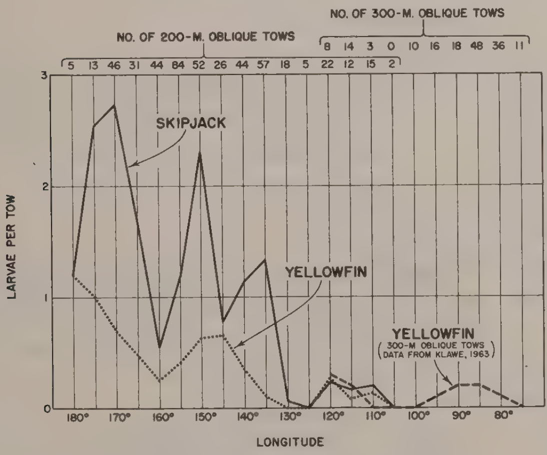

Figure 7.--Average catch of larval tunas in the central and eastern Pacific bounded by lat. 10° N. and 10° S.

The catch rates of yellowfin tuna larvae also showed a west-to-east decline, but had less local variations than those of skipjack tuna (fig. 7).

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No. 283 — SIb

CIRCULATION AND MASS TRANSPORT IN THE EASTERN NORTH PACIFIC OCEAN

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Geostrophic circulation at the surface and at depths to 4000 m has been calculated for the North Pacific Ocean for the summer of 1958. Transports have been calculated from the geostrophic velocities and compared with the mass transports calculated from wind stress data. The agreement is good when a reference level of 5000 m is used. Eastward transport in the North Pacific at 152° E has been calculated at 65×10^6 m^{3}sec^{-1}, of which 25×10^6 m^{3}sec^{-1} recirculates in the Gulf of Alaska. The surface circulation is generally eastward throughout the North Pacific Ocean, with the exception of the Alaskan Stream. The deep circulation is characterized by a clockwise gyre with its center near 168° W, 40° N. Vertical velocities indicate that upwelling is characteristic of the deep water in the eastern North Pacific Ocean below 1000 m, with maximum upward velocities occurring near 1000 m. Upward transport through the 1000 m surface in the eastern North Pacific Ocean has been estimated at 10×10^5 m^{3}sec^{-1}.

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Management of Estuarine Fisheries

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ABSTRACT

The estuarine environment, to satisfy the fishery scientist, must include the offshore zone affected by land drainage. Otherwise no major fishery resources other than oysters and some clams can be considered entirely estuarine. Nevertheless, almost two-thirds by value of the United States commercial catch and much of the marine sport catch is composed of species that spend at least a part of their lives within land-bound estuaries. Dominance of estuarine species is especially great in catches along the Atlantic and Gulf of Mexico coasts. Invertebrates are important in the commercial catch in these regions also, accounting for considerably more than 50 percent of the value of landings from Chesapeake Bay south and in the Gulf of Mexico. Estuarine fishery resources inhabit a rich but rigorous environment. Hence, they are subject to wide variations in abundance. Man's increasing fishing pressures and his other modifications of the environment place additional stresses on the resources, and man's diverse interests in the resources and their environment create difficult social-political problems. Many of the methods of dealing with these problems are antiquated and inefficient, and scientific knowledge is seldom adequate to provide clear-cut answers. The complex life-histories of most estuarine fishery resources require unusually detailed knowledge of ecology as a basis for management. Seldom have we had the facilities and resources to obtain such knowledge, and this is one reason why virtually none of our estuarine fishery resources is under effective scientific management to produce maximum sustainable yields. Solution of these problems will require improved public understanding, increased support and coordination of research and management programs, and greater opportunity for calm discussion and compromise.

INTRODUCTION

Man, of all animals, has been the most successful in developing artificial means of extending his environment. He has learned how to survive in space and in the greatest depths of the sea. Yet he remains essentially a land-bound animal, and to a considerable extent his concepts of atmospheric and oceanic circulation have been developed on a system of land-based coordinates.

This inability to sever completely our ties with the land has had a great influence on the way in which we study the ocean. For example, the principal characteristic of an estuary is that this is a place where fresh water from rivers mixes with salt water from the sea. Yet we have adopted a more restrictive definition which fixes the boundaries of an estuary with respect to the land. The definition developed by Cameron and Pritchard (1963) is illustrative:

> "An estuary is a semi-enclosed coastal body of water having a free connection with the open sea and within which the sea-water is measurably diluted with fresh water deriving from land drainage."

The only way in which the seaward boundary of an estuary can be drawn under this definition is by a line between headlands. All characteristics of the estuary based on the properties of the water (the criteria upon which a set of oceanographic coordinates should be based) intergrade along the axis of the estuary and into the open ocean, and vary seasonally and secularly with respect to fixed points on land.

Considering only the physical characteristics of an estuary, or the ecology of sessile organisms, the definition cited above is logical and useful. Measurable dilution of sea water by land drainage can be traced hundreds of miles from land in some parts of the ocean. But once this diluted water leaves the mouth of the conventional estuary, it no longer has well-defined boundaries; and it soon spreads out as a lens of relatively low density overlying the heavier and much larger mass of sea water. Here dispersal and mixing by winds and currents is much greater. However, extensive areas of the ocean in some parts of the world are influenced by land drainage. This is especially true off the shores of the northern part of North America, and this has an important bearing on United States and Canadian fisheries (McHugh, 1966a).

To the fishery scientist, who must understand the complete life history and ecology of living resources valuable to man, the existence of an arbitrary land-bound limit is not particularly useful. It is doubtful if many so-called estuarine animals observe such arbitrary boundaries. There are two general classes of animals in this sense, sessile and migratory. The total range of the sessile animals may extend beyond the limits of the conventional estuary; but if these are essentially animals of dilute, shallow waters, most individuals are truly estuarine. But most highly motile animals, especially fishes, move across these boundaries freely, and hardly any fish is an estuarine animal in the conventional narrow sense. Because many scientists have reason to hold to this restricted definition, it is perhaps best to define two estuarine zones, the "inshore estuary" based on the definition of Cameron and Pritchard (1963) and the "offshore estuary" which is that region of the open sea in which the surface waters are measurably diluted by land drainage. The offshore limit of this zone has been defined arbitrarily as the 33.5‰ isohaline (McHugh, 1966a).

ESTUARINE RESOURCES AND FISHERIES

Commercial Fisheries

Whether we adopt the broad or the narrow definition, most of our domestic marine fishery harvest in the United States is taken in estuarine waters. The commercial fishery statistics published by the United States Government do not allow precise separation of landings according to the two definitions, but this can be done fairly accurately by considering the species involved (Table 1). It is a characteristic of our domestic commercial fishery that the bulk of the catch is made up of very few kinds of fish (McHugh, 1966b). In 1963 (Lyles, 1965), the first 12 kinds in order of value made up more than 81 percent of the total catch. In order of weight the first 12 made up more than 78 percent of the catch. Most of the more important members of this group spend considerable parts of their lives in the estuaries and, for the most part, are caught in estuarine waters. By value, four of the first five are estuarine resources. Well over half of our domestic commercial fish catch is based on estuarine-dependent species.

TABLE 1.—*Species in official fishery statistics of the United States (Lyles, 1965) identified for the purposes of this paper as estuarine-dependent*

Common names	Scientific names
Alewives	*Alosa pseudoharengus, A. aestivalis*
Catfish	*Ictalurus* spp.
Croaker	*Micropogon undulatus*
Drums	*Pogonias cromis, Sciaenops ocellata*
Eel	*Anguilla rostrata*
Flounders	*Pseudopleuronectes americanus, Paralichthys* spp., *Platichthys stellatus*
Garfish	*Lepisosteus* spp.
Gizzard shad	*Dorosoma cepedianum*
Hickory shad	*Alosa mediocris*
Hogchoker	*Trinectes maculatus*
Menhaden	*Brevoortia* spp.
Salmon	*Oncorhynchus* spp., *Salmo salar, S. gairdneri*
Scup or porgy	*Calamus* spp., *Stenotomus* spp.
Sea bass (Atlantic)	*Centropristes striatus*
Sea robin	*Prionotus* spp.
Sea trout or weakfish	*Cynoscion* spp.
Shad	*Alosa sapidissima*
Silversides	*Menidia* spp.
Smelt	Families Atherinidae and Osmeridae
Spot	*Leiostomus xanthurus*
Striped bass	*Roccus saxatilis*
Sturgeon	*Acipenser* spp., *Scaphirhynchus platorhynchus*
Swellfish	*Sphaeroides maculatus*
Tautog	*Tautoga onitis*
Tenpounder	*Elops saurus*
White perch	*Roccus americanus*
Yellow perch	*Perca flavescens*
Crabs	*Callinectes sapidus, Cancer magister, Carcinus maenas*
Horseshoe crab	*Limulus* spp.
Shrimp	*Penaeus* spp., *Xiphopenaeus* spp.
Clams	*Cardium corbis, Saxidomus nuttalli, Protothaca staminea, Mercenaria mercenaria, Mya arenaria*
Mussels	*Mytilus* spp.
Oysters	*Crassostrea* spp., *Ostrea lurida*
Periwinkles	*Littorina* spp.
Bay scallop	*Aequipecten irradians*
Terrapin	*Malaclemys* spp.
Turtles	Various species
Bloodworms	Family Glyceridae
Sandworms	*Nereis* spp.

The Atlantic and the Gulf of Mexico coasts of the United States include many estuaries of the conventional kind. Long Island Sound, Delaware and Chesapeake bays, and the Sounds of North Carolina are important examples. The northern part of the Gulf of Mexico is fringed with offshore bars which enclose coastal bays and lagoons with typical estuarine characteristics. Typical fishery resources of these inshore estuaries are oysters, clams, crabs, shrimp, and a variety of coastal and anadromous fishes which use the inshore estuary as a nursery ground, or marine fishes which move into the inshore estuary seasonally. Many of these fishes remain within the influence of land drainage even when they go to sea, by staying in the extensive offshore estuarine zones of the North Pacific, the northern Gulf of Mexico, or the zone of re-

TABLE 2.—*The 12 most important kinds of commercial fish and shellfish landed in the United States in 1963*

By weight (In thousands of pounds)			By value (In thousands of dollars)		
Rank	Kind of fish	Weight	Rank	Kind of fish	Value
1	Menhaden	1,815,798	1	Shrimp	$ 70,044
2	Tuna	321,619	2	Salmon	49,012
3	Salmon	294,178	3	Tuna	40,170
4	Crabs	252,334	4	Oysters	27,105
5	Shrimp	240,478	5	Menhaden	22,386
6	Sea herring	193,604	6	Crabs	21,354
7	Flounders	176,798	7	Lobsters	18,567
8	Ocean perch	131,870	8	Flounders	15,411
9	Haddock	123,972	9	Clams	14,202
10	Jack mackerel	95,843	10	Haddock	11,705
11	Whiting	92,643	11	Scallops	10,334
12	Clams	63,403	12	Halibut	6,972
	Totals	3,802,540			$307,262

duced salinity between the Gulf Stream and the coast in the Atlantic.

Of the first six generic kinds by landed value of marine animals landed by United States commercial fishermen in 1963, five were predominantly estuarine or estuarine-dependent (Table 2). These five, shrimp, salmon, oysters, menhaden, and crabs, accounted for slightly more than 50 percent of the total landed value and about 55 percent of the landed weight of all marine and freshwater commercial landings. Some species in these groups are not estuarine animals. Although the estuarine blue crab was the most important crab landed in 1963, most of the other important crab species, particularly the king crab of Alaska, are caught in the open sea. On the other hand, many of the fish and shellfish species of lesser value are estuarine dependent. The fisheries of the Atlantic and Gulf of Mexico coasts of the United States, particularly from Long Island Sound southward, are dominated by estuarine species. Nearly two-thirds (63.7 percent by value) of the total commercial catch in the Atlantic and adjacent waters was made up of estuarine-dependent species (Table 3). Truly marine species dominate the Pacific coast commercial catch (Table 4) but there, also, estuarine-dependent species are important (45.7 percent of the total landed value in 1963).

Six basic types of gear, otter trawls, dredges, pots or traps, purse seines, tongs or rakes, and hooks or baits, in that order by value of catch, take most of the commercial catch along the Atlantic and Gulf coasts. The same six types, although not quite in the same order of importance, take most of the estuarine-dependent species (Table 3). The Pacific coast commerical fisheries also are dominated by six generic types of gear, five of which are essentially the same as those which dominate in the Atlantic and adjacent estuaries and seas (Table 5). There are some important differences. Tongs and rakes, which rank fifth in terms of value of catch on the Atlantic side (Table 3), rank very low in the Pacific (Table 5). Gill nets, which rank high in value of catch in the Pacific, are well below the first six on the Atlantic side. Otter trawls, important catchers of estuarine species in the Atlantic and Gulf, especially south of New England, take entirely marine species along the Pacific coast.

Published records (Lyles, 1965) list 212 categories of fish, shellfish, and other fishery products in United States domestic commercial fishery landings in 1963. Most of these categories represent distinct species, others include more than one species. They can be grouped under three main headings as freshwater, estuarine, or marine. This requires some duplication, because some categories include several species, not all of which fall into the same grouping. For example, the category "smelts" contains several members of the family Osmeridae which includes freshwater, anadromous, estuarine, and marine species. By allotting the 212 categories to the three main groupings, sometimes including the same category in more than one group, 36 items appear in the freshwater group, 121 in the marine, and 61 in the estuarine group.

Few, if any, of the fishes arbitrarily placed in the estuarine group are strictly estuarine fishes in the sense that they spend their entire lives within the boundaries of the conventional estuary (McHugh, 1966a). Most are anadromous like the salmons (*Oncorhynchus* and *Salmo*) or shad (*Alosa sapidissima*), or migrate seasonally from fresh water to the brackish water of the estuary like white perch (*Roccus americanus*), or migrate seasonally from the open sea to the inshore estuary like the croakers and weakfishes (*Micropogon* and *Cynoscion*). Some like bluefish, mullets, and pompano, might also be included. They were omitted, however, because they do not use the inshore estuary as a spawning or nursery ground, and the inshore movements of adults are transitory. The estuarine crustacea are not limited in their distribution by the conventional boundaries of the estuary so far as we know, although most individuals of a typical estuarine animal like the blue crab (*Callinectes sapidus*) in Chesapeake Bay probably never cross these boundaries. Some of the estuarine molluscan shellfishes probably fit most closely to the definition of a truly estuarine resource, for although the distribution of a species may transcend the conventional boundaries, an individual of that species, once it has renounced planktonic life, is bound for the rest of its existence to the immediate vicinity or the exact spot on which it settled.

Into this arbitrarily selected group of estuarine fishery resources fall many of the most valuable commercial fishery resources landed by our fishermen, including shrimp, which in total value of landings are the most important commercial seafood caught by United States fishermen; menhaden, the most important in terms of weight and fifth in dollar value; salmon, second in value in 1963; and oysters, fourth in value. Of the truly marine species, only the tunas rank among the first five by total value of landings.

Estuarine species dominate commercial fishery landings along the Atlantic and Gulf of Mexico coasts of the United States. This dominance is especially striking if the New England catch is omitted (Table 6). Landings in New England and along the Pacific coast are primarily truly marine species. It is interesting also that invertebrates are dominant contributors to the value of the catch along the Atlantic coast and in the Gulf of Mexico. New England and Pacific coast landings are predominantly finfishes (Table 7), although invertebrates dominate landings in some of the New England States also: lobsters in Maine and New Hampshire and lobsters and mollusks in Connecticut (Table 8). But the important landings of groundfish in Massachusetts and Rhode Island, in which finfish predominate, reduce the relative value of the invertebrate catch in the fisheries of New England as a whole.

TABLE 3.—*Value of the catch by gear along the Atlantic and Gulf of Mexico coasts of the United States in 1963*

[In thousands of dollars]

Gear	Rank	Value of total catch	Value of estuarine resources in total catch	Estuarine species as a percentage of the total catch
Otter trawls	1	$111,865	$ 75,906.7	67.8
Dredges	2	32,469	15,777.6	48.6
Pots and traps	3	23,510	6,252.0	26.6
Purse seines	4	23,234	22,171.4	95.4
Tongs and rakes	5	14,888	14,753.0	99.1
Hooks and baits	6	11,138	4,349.8	39.0
Gill nets	7	5,672	2,447.1	43.1
Pound nets	8	2,937	2,338.6	79.6
Hoes and forks	9	2,723	2,722.2	99.9
Haul seines	10	2,506	1,372.8	54.8
Stop nets	11	1,455	3.2	0.2
Trammel nets	12	1,160	545.1	47.0
By hand	13	1,048	1,047.2	99.9
Scrapes	14	687	686.8	99.9
Dip nets	15	566	535.1	94.5
Floating trap nets	16	530	0.0	0.0
Other gears		1,301	497.7	38.2
Totals		$237,696	$151,406.3	63.7

Recreational Fisheries

It is more difficult to get precise figures for the marine sport fish catch, and the available literature is contradictory, but it is reasonable to assume that most of this catch comes from estuarine waters. Clark (1962) listed 75 marine sport fish species or groups of species for the entire United States coast, excluding Hawaii. None of these dominated the sport catch by weight as menhaden dominate the commercial catch. Indeed, few species or groups of species accounted for more than 5 percent of the total. The first 10 in order of total weight landed, according to Clark's figures, made up about 52 percent of the total catch. In order of importance by weight these were: sea trouts, drums, groupers, flat-

TABLE 4.—*Weight and value of estuarine species in the Pacific coast catch in 1963*

Rank	Kind of fish	By weight (in thousands of pounds)	By value (in thousands of dollars)
1	Salmon	294,177	$ 49,011
2	Dungeness crab	24,863	4,306
3	Oysters	9,791	2,483
4	Smelt	1,663	132
5	Shad	1,503	104
6	Steelhead	1,353	395
7	Sturgeon	401	51
8	Hard clams	386	183
9	Striped bass	69	10
	Totals	334,206	$ 56,675
	Grand totals	1,116,733	$124,105

TABLE 5.—*Value of the catch by gear along the Pacific coast of the United States in 1963*[1]
[Landed value in thousands of dollars]

Type of gear	Rank	Value of total catch	Value of estuarine resources in total catch	Estuarine species as a percentage of the total catch
Purse seines	1	$ 52,660	$22,700	43.1
Hooks and baits	2	31,730	12,192	38.4
Gill nets	3	14,587	14,116	96.8
Pots and traps	4	12,348	4,431	35.9
Otter trawls	5	7,669	0	0
Dredges and by hand	6	2,449	2,433	99.4
Diving outfits	7	626	0	0
Harpoons	8	589	0	0
Haul seines	9	393	199	50.6
Shovels	10	347	108	31.1
All others	11	707	512	72.4
Totals		$124,105	$56,691	45.7

[1] Hawaii not included.

fishes, jacks, striped bass, sharks, spearfishes, bluefish, and porgies.

Although it is recognized that the saltwater sport fisheries of the United States are important and that they have grown rapidly in the past 20 years, we still have only a general idea of their magnitude along the entire sea coast of the United States. It would appear on the basis of the best possible estimates that the total catch by sport fishermen from the ocean around our coasts in 1960 was about 11 percent of the weight of the total commercial catch. This estimate does not include what may also be a substantial recreational harvest of certain invertebrates, especially clams, crabs, and shrimp. Thus, it is well established from what are considered to be conservative estimates that the saltwater sport fisheries support an extremely important commercial enterprise, based almost entirely upon estuarine resources. It is important that we develop the best possible methods of measuring catch and effort in this fishery, and of estimating its economic value.

It is most difficult to obtain accurate measures of sport fish catches. No national system of gathering complete statistics has been established, not so much because the importance of such an activity is not recognized, but rather because it would be prohibitively expensive. As Walford (1965) has pointed out, the necessary statistics must be obtained by a scientifically designed sampling plan. Precise application of the principles of population dynamics in management of marine sport fisheries probably never will be possible, because measures of catch and effort must be gained from incomplete data. As Walford has said: "it seems most likely that any regulation of the catch of sport fishermen would have to be based more on well informed judgment than on mathematical calculations."

Although some States have made fairly accurate estimates of their marine sport fish catches for certain years, and California routinely collects statistics from the party boat fishery, the only estimates for the entire coast of the United States have been made on the basis of interviews and questionnaires from a small sample of the total population. The errors inherent in such methods are well known, and it is generally conceded that they are apt to give exaggerated estimates of the catch (Abramson, 1963; Carlander et al., 1958; Stroud and Jenkins, 1962). The most comprehensive national surveys yet made were done by the Bureau of the Census in 1955 and 1960 (Clark, 1962). These provided estimates only of the *numbers* of each species caught and the total weight was derived from the estimated average weight of each species in the angler's catch. The problems involved in estimating weights by this method are well illustrated by comparing the average weights used by Miller and Gotshall (1965) and Clark (1962). Recognizing these difficulties, it is not surprising that two estimates derived from the 1960 Census data were widely different. Clark (1962) concluded that the total marine sport fish catch in 1960 was about 1.4 billion pounds. A report prepared for the Outdoor Recreation Resources Review Commission

(Anonymous, 1962)[1] concluded that the 1960 national marine sport fish catch was about 590 million pounds. Stroud and Jenkins (1962) reviewed both estimates and concluded that the lower estimate was more realistic. An even more exaggerated estimate of the salt water sport fish catch (11.25 billion pounds a year) was published by error recently (Anonymous, 1966).

Walford (1965) stated that the nationwide survey conducted by the Bureau of the Census provided data from which it was estimated that the 1960 catch by United States salt water anglers was over 1.4 billion pounds. He concluded that most marine food fish species which can be caught on hook and line are yielding much larger catches to anglers than to commercial fishermen. This conclusion is open to doubt for several reasons. The Outdoor Recreation Resources Review Commission (ORRRC) estimate (*loc. cit.*) of nearly 600 million pounds has been recognized as more realistic. The United States commercial catch statistics do not represent the entire commercial catch of several important species off our coasts, such as salmon, ocean perch, rockfishes, flounders, haddock, cod, scup, pollock, and others which are taken also by foreign fishermen. Moreover, the species included in Walford's tables were those for which the estimated catch by anglers or by commercial fishermen was 10 million pounds or more. If the more conservative and reasonable estimate of total salt water sport fish catch had been used, it is probable that several of the sport fish species would not have been included in these tables. The published sport fishing data are not sufficiently detailed to permit recalculation of the total weight of each species caught, but an approximation can be reached by adjusting each figure by the ratio of the ORRRC estimate to the estimate cited by Walford. On this basis, in Walford's tables the number of sport fish varieties listed for the Atlantic coast would be reduced from 25 to about 13; the Gulf of Mexico list would decrease from 11 to about 5; and the Pacific coast list, from 7 to about 2.

TABLE 6.—*Importance of estuarine species in the United States marine fish catch in 1963*

	Landed value of catch in thousands of dollars		Percent estuarine
	Estuarine species	Total	
New England	$ 7,376	$ 68,289	9.3
Middle Atlantic	15,025	21,345	70.5
Chesapeake	29,344	29,804	98.4
South Atlantic	17,070	19,468	87.7
Gulf of Mexico	87,544	98,790	88.6
Pacific Coast[1]	56,675	124,105	45.7

[1] Hawaii not included.

No estimates are available for recreational catches of invertebrates. In some areas substantial recreational catches of crabs, clams, and shrimp are made. It is unlikely that these catches are greater than 20 percent by weight of the total catch of these groups.

Comparison of Commercial and Recreational Catches

It is interesting to take the detailed listing of sport catches in Clark's (1962) tables and the commercial catches in Power (1962) and to compare the percentages of the total harvest of each kind of marine animal taken by anglers or by commercial fishermen. The precision of the sport fish estimates, when each is reduced arbitrarily by the ratio 0.59/1.4, is questionable, and the comparison can be regarded only as indicative. But the result is essentially the same whether Clark's or the ORRRC estimate is used. As illustrated by Tables 9 to 11, the conclusion is clear that with some notable exceptions direct competition between recreational and commercial fisheries is not great. The strikingly biomodal nature of the distributions is illustrative. When the frequency distributions in Table 9 are converted into total weights, as in table 10, it is clear that although the marine sport fish catch is impressive, it does not yet rival the total marine commercial catch in magnitude as Walford's (1965) paper seems to infer.

Many attempts have been made to estimate the economic value of the marine fisheries, recreational and commercial. Commercial catches usually are expressed as the price paid to fishermen when the catch is landed. It is possible also to compute the retail value of the commercial catch. The value of sport fisheries usually is calculated from the money spent by fishermen for such items as travel, food, hotel rooms, fishing gear and supplies, boat rental and fuel. This is an entirely different approach, and there is some argument as to whether all such expenses should be allocated to the pursuit of recreational fishing. At any rate, this method produces a valuation which can be expressed in terms of dollars. All too often the next step is entirely fallacious. We are so accustomed to adding dollars that it appears to be entirely logical to add these two values, derived in completely different ways, to arrive at a total value for the combined commercial and sport fisheries. Actually, no one has succeeded in deriving dollar values for sport and commercial fisheries which are comparable or additive in an economic sense. This important fishery problem remains to be solved.

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[1] It is appropriate to give credit to the authors of this report. They were Willis King, Jack Hemphill, Albert H. Swartz, and Karl Stutzman of the Bureau of Sport Fisheries and Wildlife.

SOME PROBLEMS OF ESTUARINE FISHERIES

Domestic Problems

Virtually all species identified for the purpose of this discussion as estuarine resources are caught within United States territorial waters. The only important exception is the shrimp fishery of the Gulf of Mexico, in which a part of the catch is made in international waters. Probably not more than 25 percent of the total Gulf catch is made outside United States territorial waters, and many of those caught beyond the three-mile limit probably originated in United States estuaries or nearshore waters and had migrated offshore as they grew. Many of those species listed as marine species also were caught in the estuaries or within the three-mile limit. Thus, there is no doubt that the estuaries are an important seasonal or permanent habitat for most of our most valuable American fishery resources, and that wise use of these resources demands preservation and enhancement of the favorable characteristics of the estuarine environment and rational management of the fisheries therein.

Because they are conducted primarily within territorial waters almost all the fisheries of the United States come under the jurisdiction of the individual States, for the Federal Constitution does not reserve the right to manage the fisheries in United States territorial waters. The fisheries of the inshore estuary, by their very nature, are regulated entirely by the States. Many States carry on research designed to provide a fund of information for use in developing and improving their management programs. The role of the Federal Government in contributing to this encyclopedia of knowledge is to undertake research and development activities which are beyond the capabilities of an individual State for various reasons, or which are of general interest to several States. It is for these reasons that the Atlantic States Marine Fisheries Commission (ASMFC) and the Gulf States Marine Fisheries Commission (GSMFC) named the United States Fish and Wildlife Service as their primary research agency.

Estuarine waters and their living resources have a variety of uses, many of which are potentially incompatible. In the absence of a fairly clear understanding of the effects of one such use upon the other uses, decisions as to the proper balance to be achieved between conflicting interests and the ways in which such decisions are implemented must be made in purely arbitrary ways. If the issues are likely to affect a large portion of the local population, or if it is thought that they will, decisions usually are made through a series of power plays which involve economic, recreational, aesthetic, and social-political forces. The emotional furore which often surrounds such problems is not conducive to clear thinking or statesmanlike disposition of the problem. The better the available fund of basic information about the response of estuarine organisms to naturally and artificially induced changes in the environment, the better can controversies be resolved in the best interests of the fisheries. Unfortunately, the need for information seldom is recognized until a problem already exists. The complexities of ecological relationships cannot be unraveled easily, and there is no such thing as a "crash program" in ecology. Instead, there are some rather high thresholds of financial support of research, below which

TABLE 7.—*Importance of invertebrates in the United States marine fish catch in 1963*

	Landed value in thousands of dollars			Percent invertebrates
	Fishes	Invertebrates	Other	
New England	$ 37,051	$31,109	$129	45.5
Middle Atlantic	10,830	10,508	7	49.3
Chesapeake	8,412	21,366	26	71.7
South Atlantic	9,019	10,428	21	53.6
Gulf of Mexico	24,576	74,200	14	75.2
Pacific coast[1]	106,322	17,223	560	13.9

[1] Hawaii not included.

TABLE 8.—*Importance of invertebrates in the New England marine fish catch in 1963*

	Landed value in thousands of dollars			Percent invertebrates
	Fishes	Invertebrates	Other	
Maine	$ 5,775	$15,341	$100	72.4
New Hampshire	39	404	0	91.2
Massachusetts	28,544	12,661	29	30.0
Rhode Island	2,404	1,745	0	42.1
Connecticut	289	958	0	76.8

an understanding of cause and effect may never be attained. Most failures in fishery management can be attributed to lack of scientific knowledge or failure to make use of knowledge that is available. The research required to solve any major problem of estuarine fisheries should be started long before the problem arises, if that problem is to be solved immediately. Indeed, if we ever reach the stage of reasonably complete understanding, most problems should be anticipated and solved before they arise.

Physical factors of natural origin. Because most estuaries are relatively shallow, or contain large areas of shallow water, the general environment of estuarine animals is quite unlike the conservative environment of the open sea. Relatively large variations in temperature and salinity occur over short time intervals. Winds and currents transport large quantities of silt and larger particles, sometimes causing large-scale erosion of shorelines and bottom, depositing the eroded materials elsewhere with marked effects upon the biota. The amounts of suspended materials in the water vary with land drainage and other disturbing factors. Thus, the typical estuary is a highly dynamic system in constant flux, with which the biota must constantly struggle to maintain themselves. Catastrophic mortalities of marine life are not uncommon in estuaries, and the sublethal effects of the unstable physical environment are undoubtedly equally variable. Consequently, estuarine animals are subject to wide variations in abundance. Although this is so evident as to be a truism, not requiring rigid scientific demonstration, we know almost nothing about cause and effect in the estuarine system. We understand a few of the physical variables which are operating and can see some of their grosser effects. There probably are many more physical factors which we neither see nor recognize as important forces. Moreover, these variables, known or unknown, probably react and interact in a wide variety of ways, affecting the biota by reinforcing each other, countering each other, or operating only when they exceed certain threshold levels.

Physical factors of human origin. The same kinds of effects are produced by human activities. Construction of dams and dredging of channels cause variations in temperature or salinity of the water or may alter these characteristics permanently. Dredging and other engineering works can produce the same effects as winds and currents, causing temporary or permanent changes in bottom topography or character of water flow. More disturbing, because they are apt to be progressive in their adverse effects on the dynamic equilibrium of physical forces, are domestic and industrial pollution, and destruction of salt marshes, which alter the characteristics of the water and of the bottom in many ways. The effects of most human activities are indistinguishable from the effects of natural variables, unless the changes are so catastrophic that the cause can be identified beyond reasonable doubt. Few of us, even the best scientists, can distinguish between the sublethal effects of variables of natural or human origin. Under such circumstances it is human nature to lay the blame on man, or at least to take the more sophisticated view that if we are not sure, each alteration of the natural environment by man should be considered as having an adverse effect on the biota until can be proven otherwise.

TABLE 9.—*Frequency distributions of ratios of estimated total weight of U. S. saltwater sport fish catch to total weight of saltwater commercial fish catch*[1]

	Marine sport fish catch as a percentage of total marine catch:				
	0–19.9	20–39.9	40–60	60.1–80	80.1–100
Finfishes only:					
Using Clark's estimates	15	3	5	3	19
Using ORRRC estimates	18	5	2	5	15
Including major invertebrates:					
Using Clark's estimates	20	3	5	3	19
Using ORRRC estimates	23	5	2	5	15

[1] All sport fish species for which Clark (1962) estimated a total catch of less than 10 million pounds were lumped as "all others," unless a species was also a major item in the commercial catch. All commercial species for which the 1960 catch (Power, 1962) was less than 10 million pounds were lumped as "all others," unless a species was also a major item in the sport catch. Table 11 lists the species or groups of species used.

Biological factors. The biological consequences of the integration of all these forces are there for everyone to see. Yet few of us read the evidence correctly or understand what is meant by the environment of a marine organism. It is common practice to measure temperatures, salinities, or some other easily determined quantities as if they were adequate descriptors of the surroundings of the organism which determine its survival, growth, and general health. But these are only gross criteria of the true environment, as Galtsoff (1964) has pointed out. It is not unreasonable to conclude that temperature, salinity, and certain other variables have important influences upon the biota, but it does not follow that we understand how these or other forces operate upon the organism in its natural environment. The evidence which is so clearly laid before us, yet which we so often fail to note, is the short- and long-term variation in abundance, movements, growth, survival, and a variety of other biological characteristics, which vary independently from species to species with no evident interdependence. This means that there are other factors operating, which we have not measured, or that each species responds to each factor in its own way. Whenever ecologists have attempted to demonstrate simple relationships between the natural environment and a marine species or stock, future events have proven them wrong. In addition to the complex interactions between the physical environment and marine populations, there are infinitely more complicated interrelationships within and between populations, species, and associations of living things.

By the very act of fishing, man disturbs the estuarine environment. This is primarily a biological influence, because it removes certain species selectively, hence alters the dynamic equilibrium between the biota. It is common to conduct studies of the effects of fishing as if the interactions between species and between the environment and species did not exist. This approach has been reasonably successful with some stocks of marine animals, notably fur seals in the North Pacific and Bering Sea, halibut in the Gulf of Alaska, yellowfin tuna in the eastern tropical Pacific, and baleen whales in the Antarctic. But this merely demonstrates empirically that for these species the fishery is apparently the dominant force determining population size over the historic range of fishing intensity and time period of the study.[2] It probably is significant that these are all strictly marine species which live in a conservative environment, less subject to large and sudden physical changes. I can cite no comparable example of an estuarine fishery in which a close relationship between fishing effort and maximum sustainable yield has been demonstrated so clearly. This statement ignores a substantial accumulation of scientific and technological information on oyster production, which is quite adequate to rehabilitate the oyster industry in most areas and to maintain much higher sustainable yields, if social-political barriers could be removed. But oyster growing is a form of farming or animal husbandry, in which certain property rights have been established and are recognized by tradition in many areas. This is quite a different situation from the common-property characteristic, and the hunting technology, of the typical finfishery or of most other invertebrate fisheries.

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[2] It is not intended to infer that these fisheries are under effective management, but only that there is a demonstrated relationship between fishing intensity and yield and a demonstrated management goal that would produce the maximum sustainable yield. At the time of writing the fur seal and halibut fisheries are under reasonably effective management schemes, the yellowfin tuna and Antarctic baleen whales are not.

Fishing operations may change the physical characteristics of the environment also, either temporarily or permanently. The adverse effects of such modification usually, although perhaps not always, are overestimated by those unfamiliar with the operation of fishing gear. For example, complaints sometimes are received that purse seines, haul seines, or trawls damage spawning and nursery grounds or shellfish bottoms. Usually such complaints are unwarranted, although it should not be assumed that improper operation of such gears could not do damage. Seldom does one fisherman set out deliberately to destroy the livelihood of another fisherman. When one fishing operation is causing damage or is likely to cause damage to another, it usually is a simple matter to resolve the problem. Hydraulic dredges can cause substantial changes in the characteristics of the bottom which may, under certain circumstances, affect other resources (Manning, 1957). In these circumstances, also, the problem usually can be resolved by careful study and appropriate compromise, with economic advantage to the fisheries as a whole.

The complex interactions between organisms or between populations of organisms are not well understood. Various scientists have speculated on the effects of competition, predation, disease, and other biological phenomena upon the abundance of commercial fishery resources. Some of the best documented examples are to be found in the literature on oysters and oyster growing. For example, Carriker (1955) believed that oystering practices prevalent along the Atlantic coast of the United States probably have stimulated the destructive activities of the oyster drills *Urosalpinx* and *Eupleura*. Korringa (1952) believed that bad oystering practices could aggravate losses and that survival could be improved by using accumulated experience to modify oyster farming practices. Andrews (1965) said that concentrations of oysters stimulate epizootics of *Dermocystidium marinum*, and suggested methods of oyster planting which may check mortalities caused by *Dermocystidium*.

Recent work in California cited by Roedel (1966) and Murphy (1965) refers to the well-documented reversal in abundance of Pacific sardine (*Sardinops caerulea*) and anchovy (*Engraulis mordax*). Estimates of the magnitudes of the adult populations of these two species show that the sardine dropped from about 4 million tons in 1932 to about 0.2 million in 1959, whereas the anchovy increased from about 1.3 million in 1941 to nearly 5 million in 1957. Ahlstrom (1965) observed that anchovy larvae in the plankton, which were only 3.3 times as numerous as sardine larvae in 1951, increased progressively in abundance until in 1962 the ratio was 80 to 1. The State has consistently opposed catching of anchovy for reduction to oil and meal, but in 1965 an experimental fishery was authorized with the object of measuring the effect of fishing on the anchovy stocks, and the consequent interaction between anchovy and sardine abundance. The progress of this experiment will be watched with great interest. McHugh (1966a) speculated upon the possibility of a similar inverse relationship in abundance between blue crabs and menhaden in Chesapeake Bay. Even if the mechanism for such interactions exists it is too much to expect that exact correlations will be demonstrated, for this would require satisfaction of the assumption that significant disturbing effects are produced neither by physical factors nor by other members of the biota. Such assumptions represent vast oversimplifications of highly complex series of phenomena.

Social and political factors. Each of these three kinds of forces, physical factors of natural origin, physical factors of human origin, and biological interactions, produces a spectrum of effects, the end results of which may be indistinguishable one from another. Occasionally the result is spectacular and widespread so that it is clearly evident to a large number of people, such as a massive

TABLE 10.—*Total estimates of saltwater catch in millions of pounds by United States recreational and commercial fishermen of the species or groups of species included in Tables 9 and 11*

	Sport catch as a percentage of total catch:				
	0–19.9	20–39.9	40–60	60.1–80	80.1–100
Finfishes only:					
Using Clark's (1962) estimates	3,525.4	492.8	454.3	127.3	973.6
Using ORRRC estimates	3,987.7	335.8	29.4	138.6	361.1
Including invertebrates:					
Using Clark's estimates	4,273.8	492.8	454.3	127.3	973.6
Using ORRRC estimates	4,666.1	335.8	29.4	138.6	361.1

fish mortality, an extensive bloom of plankton, or a sudden increase or decline in abundance or availability of a popular commercial or recreational resource. More often, the effects are less spectacular and come more slowly to public attention. There should be little wonder, then, that cause and effect are often attributed to factors which were not responsible.

The principal mechanism for regulating fisheries in most States is through action in the State Legislature. In some States control is delegated to local governments, counties, or sometimes even towns. A few States have recognized the problems connected with legislative control and have vested various degrees of responsibility in fishery commissions or departments of conservation, which are insulated more or less from direct political influence. Even the best of these systems creates problems for the nation as a whole, however, for most coastal resources, even typically estuarine forms, migrate freely from the waters of one State to another. The coastal States, recognizing the need for coordination, yet unwilling to relinquish the entire responsibility to the Federal Government, have entered into compacts. Two of these compacts, executed by the Atlantic coastal States and the Gulf of Mexico coastal States, respectively, include the Federal Government as a partner in certain of their activities. The third compact, with membership drawn from the Pacific coastal States, includes the Federal Government only in the role of observer or as a participant by invitation. The relationships between the States and the Federal Government through the mechanisms of the Commissions established under these compacts and in other ways have been described in detail (McHugh, 1966b). The objectives and accomplishments of one of these Commissions have been reviewed by McHugh (1963a). Progress toward the goal of rational and coordinated management of the nation's estuarine fisheries has been slow and uneven. There are two principal and interlinked basic reasons for this slow progress, a lack of adequate scientific understanding of the ecology of estuaries, and a bewildering array of restrictive legal codes which reflect public misunderstanding of the requirements for good management. Consequently, with few exceptions, our estuarine fisheries are primitive and inefficient technologically and economically. Some of the most important estuarine resources, notably oysters, have been needlessly overexploited and mismanaged because the necessary remedial steps are blocked by laws honestly intended to protect and rehabilitate the resource (McHugh, 1963b).

International Problems

Rapid growth of world fisheries and increasing activity by foreign fleets off our coasts have directed the attention of some segments of our industry toward these new threats to their livelihood. These new fisheries may compete with historic domestic fisheries for resources valuable to us. They may develop new fisheries on species or stocks which we do not now exploit. Both kinds of fishery can disturb the ecological balance of our coastal waters and can have important effects upon our harvest. Few of our estuarine fishery resources are affected seriously by foreign fishing now, but we can expect these problems to grow. Our ability to solve them will depend on our knowledge of the biology of the species and the characteristics of the coastal water circulation. Generally speaking, biological research has played a much more important part in the affairs of the international fishery commissions than it has in developing our domestic fishery laws.

The principal fishery resources affected by foreign fisheries off our shores are salmon, halibut, and king crab in the Bering Sea and Gulf of Alaska; tunas and billfishes in the Pacific and the Atlantic; and groundfish in the Northwest Atlantic. Of these, only salmon are an estuarine resource, and they are not in the inshore estuaries when they become vulnerable to foreign fishing. To a considerable extent our domestic salmon management programs have been aided, and the resource reserved for American fishermen, by incorporation of the Principle of Abstention in the provisions of the International Convention for the High Seas Fisheries of the North Pacific Ocean. This Principle provides that if more intensive exploitation will not provide a substantial increase in sustainable yield of a stock of fish which is harvested by one or more contracting parties, and if the fishery is regulated by these parties on the basis of extensive scientific research to maintain or increase the maximum sustainable yield, other contracting parties not engaged in the fishery shall agree to abstain from harvesting the resource.

Menhaden have not been taken by foreign fleets yet, and there is some question whether menhaden enter international waters in sufficient quantity or with sufficient regularity to support a fishery. Other schooling fishes off our shores are vulnerable to foreign fishing, and a heavy fishery on the Continental Shelf might have profound influences upon our estuarine resources. We need to improve understanding of the ecology of the coastal waters if we are to reach reasonable understanding with other nations on managing coastal fisheries of joint interest.

To understand fully the estuarine environment and its effects upon the fishery resources may require very broad investigations. For example, it is unlikely that we will understand the circulation of the Gulf of Mexico thoroughly until we know how the Gulf is affected by the currents of the entire tropical Atlantic. Studies in the Pacific have made it clear that the circulations of the atmosphere and the ocean are intimately related and that one can have profound effects upon the other (Sette and Isaacs, 1960). Bennett (1966) has shown that the Azores High over the Atlantic Ocean affects the oceanography, and presumably the tunas, of the eastern tropical Pacific. Our knowledge of the influence of these changes upon the living resources of the sea is still very imperfect. We must improve our knowledge of the global atmospheric and oceanic circulation if we are to develop international management agreements that will keep pace with the rapid development of high seas fisheries.

Where national differences in economic and political objectives make it difficult for nations to agree upon rational management measures the results can be extremely frustrating. Such problems have plagued the International Whaling Commission for years. Gulland (1965) has made the interesting suggestion that these difficulties might be solved by placing whale resources under control of the United Nations. Whaling interests would receive compensation for agreeing to refrain from killing overexploited stocks until the natural productivity of the resource was restored. This proposal has the appeal of elegant simplicity, but it presents some enormous difficulties in execution. Christy and Scott (1965) have discussed a somewhat similar proposal, among others, for worldwide management of marine fisheries, and have identified some of the problems. Such arrangements for comprehensive international control, if they come about, will have an important bearing on fishery management in territorial waters.

MANAGEMENT OF ESTUARINE FISHERIES

What are the objectives of fishery management in estuaries? At first glance the answer appears to be simple: to ensure the maximum catch today and forever. Like many generalizations about natural phenomena this is a gross oversimplification. The objectives are different according to the point of view. The commercial fisherman, the sport fisherman, the economist, and various other interested parties, each has a different view, as will be discussed in the sections to follow. These differences often are incompatible unless the

TABLE 11.—*The species of marine sport fishes or groups of species falling within each frequency band in Tables 9 and 10*

Frequency band	Kind of resource	Clark's estimates	ORRRC estimates[1]
Marine sport fish catch 0–19.9 percent by weight of total marine catch	Finfishes	Menhadens Tunas Sea herrings Salmons Ocean perch & Rockfishes Haddock Whiting Jack mackerel Pacific sardine Alewives Halibut Thread herring Sablefish Butterfish Unclassified (Misc.)	Menhadens Tunas Sea herrings Salmons Ocean perch & Rockfishes Flounders Haddock Whiting Jack mackerel Pacific sardine Alewives Halibut Mullets Mackerel Thread herring Sablefish Butterfish Unclassified
	Shellfishes	Shrimps Crabs Oysters Clams Scallops	Shrimps Crabs Oysters Clams Scallops
Marine sport fish catch 20–39.9 percent by weight of total marine catch	Finfishes	Flounders Mullets Mackerel	Scup Cod Pollock Spot All others
Marine sport fish catch 40–60 percent by weight of total marine catch	Finfishes	Scup Cod Pollock Spot All others	Snappers Black sea bass
Marine sport fish catch 60.1–80 percent by weight of total marine catch	Finfishes	Snappers Catfishes (marine) Black sea bass	Catfishes (marine) Striped bass Spanish mackerel Croakers Kingfishes
Marine sport fish catch 80.1–100 percent by weight of total marine catch	Finfishes	Sea trouts Striped bass Spanish mackerel Croakers Groupers Kingfishes Sharks Bluefish Jacks Black drum Red drum Spearfishes Bonitos Barracudas Grunts Tautog Yellowtail Cabezon & sculpins Tarpon	Sea trouts Groupers Sharks Bluefish Jacks Black drum Red drum Spearfishes Bonitos Barracudas Grunts Tautog Yellowtail Cabezon & sculpins Tarpon

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[1] Derived arbitrarily by using the factor 0.42 (the ratio 0.59/1.4).

various interests are willing to seek the facts and to reach an agreeable compromise.

Management of estuarine fisheries requires scientific research and administrative arrangements to put the scientific knowledge to work. Research results, to be effective, must be capable of translation into terms the layman can understand and support. Administrative arrangements must take into account the various interests and conflicts and must attempt to arrive at reasonable and mutually acceptable compromises.

Scientific Aspects

Shortly after the close of the Civil War the fisheries of New England, particularly the States of Massachusetts and Rhode Island, were believed to be declining. The popular belief was that traps and pound nets were overfishing the resources (Baird, 1873). Special studies made by the legislatures of the two States reached quite contradictory conclusions. Local concern was sufficiently great to persuade the Federal Government to make an investigation, and in 1871 Dr. Spencer F. Baird began studies based at Woods Hole, Massachusetts, which led eventually to formation of the present United States Fish and Wildlife Service. Dr. Baird's studies convinced him that fishing activities and natural causes were contributing to the scarcity of fish, and he recommended regulation of pound-net fishing as a means of restoring former abundance. The charts accompanying his report do not leave the impression that fishing effort was very great. From our present vantage point, it appears very unlikely that the resources were being overfished 95 years ago. Yet Dr. Baird, on the basis of limited scientific studies, drew upon his scientific knowledge and experience to suggest that the causes of such problems were complex and involved natural as well as man-made forces. His views are well supported by our superior knowledge today.

Indeed, interactions between natural and artificial forces are the principal sources of difficulty in managing fisheries, especially those of estuarine waters. Two major models, termed the logistic and the dynamic-pool models by Dickie (1962), are used as a basis for scientific fishery management. Regulations based on both models, but especially the logistic, will work best if fishing is the only cause of variation in abundance or availability of fish. But we know that this is seldom true. One of the reasons for the success of the Inter-American Tropical Tuna Commission (Schaefer, 1957) in obtaining a fairly accurate measure of the maximum sustainable yield of yellowfin tuna in the eastern tropical Pacific has been that recruitment does not vary greatly from year to year. The logistic model assumes that recruitment is constant, and this assumption has been reasonably well met by the yellowfin tuna resource in the area of interest, at least during the period under study.

On the other hand, application of empirical methods based on past experience to the management of salmon runs is not a very precise method of management. For example, if it were decided to base regulation of a salmon fishery entirely on the historical relationship between numbers of spawners and the return of the progeny as adults, the so-called escapement-return relationship, the management program would not be signally successful in maintaining the maximum sustainable yield. Good examples are provided by the work of the International North Pacific Fisheries Commission (Jackson, 1962). Although large spawning escapements on the average produce large returns and small escapements small returns, the influence of environment is so variable that the relationship does not have precise predictive value.

Moreover, it is not possible to say during the fishing season, when decisions must be made as to how many fish should be allowed to reach the spawning grounds, whether conditions will be favorable for survival of eggs and young. Fortunately, our knowledge of the ecology of Pacific salmon is improving rapidly as a result of substantial investments in research in the last 25 years, and our ability to manage salmon runs is improving thereby. As our management skills improve, however, domestic emphasis has been shifting to the threat of indiscriminate foreign fishing, which can nullify our rapidly improving management skills unless it is checked.

Pacific salmon is the only United States estuarine fishery resource under reasonably effective scientific research and management. The history of salmon management demonstrates the merit of making the best use of available information, even if this information is incomplete. Our ability to manage salmon resources is far from perfect, but in most areas the United States and Canada are making good use of accumulated scientific knowledge to maintain and in some cases to improve salmon runs. The cost of research and management has been high, and there is no doubt that we are spending more money on this resource than any other fishery stock. This merely serves to illustrate that estuarine fishery research and management are difficult and costly. Although some people have concluded that we are spending too much effort on salmon to the neglect of other important fisheries, the correct conclusion probably is that salmon research will succeed because we *are* giving it reasonably adequate attention and that research on most other estuarine resources must be supported more generously if management is to succeed.

Enactment of Public Law 81–681, The Dingell-Johnson Act of 1950, as amended, Public Law 88–309, the Commercial Fisheries Research and Development Act of 1964, and Public Law 89–304, The Anadromous Fish Act of 1965, were steps in the direction of Federal-State cooperation to this end, for research and management of estuarine fisheries must be a joint venture of the Federal Government and the States. It is important for all concerned to recognize that the magnitude of research effort must be measured not in terms of the value of a particular resource, but in terms of the difficulty of the management problems. The relatively modest expenditures which have provided information adequate to manage halibut, yellowfin tuna, fur seal, and whale fisheries perhaps have led to the mistaken view that such levels of research support are adequate for any fishery.[3] Management of most estuarine fisheries is much more difficult because these resources are subject to wide variations in abundance not only from fishing and other human activities but also from natural causes. This requires much broader research programs to provide the information needed for management. Such research may be five to ten, or more, times as costly as halibut or fur seal research.

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[3] As noted earlier, although information is available for management of yellowfin tuna in the eastern Pacific and baleen whales in the Antarctic, these resources are not being managed effectively.

The effect of fluctuating recruitment upon a fishery resource under management for maximum sustainable yield according to the models mentioned above has never been examined adequately. It is interesting to speculate upon an ideal fishery conforming to the logistic model and exploited by a fishing fleet which exerts just the effort necessary to take the maximum sustainable yield. As long as recruitment remains constant, such a fishery can continue to harvest the maximum sustainable yield forever if fishing effort remains constant. If nature intervenes by creating conditions unfavorable for survival of young, the supply of recruits to maintain the fishery will dwindle. Responding to this decrease in abundance, the fishing fleet may well increase its effort, taking a larger percentage of the total resource. Even if fishing effort remains constant, it may be harmful to the resource to continue to take the same proportion of a declining stock as was taken in the equilibrium condition. Changes in fishing effort tend to lag behind development of a fishery and fluctuations in abundance in somewhat the same way that abundance of a predator may lag behind the abundance of its prey. Thus, the fishery probably will overexploit a decreasing resource and will underexploit increases in abundance. The effects of overfishing on a resource which is declining from natural causes may be permanent and disastrous. As yet, we know very little about such phenomena and can only speculate on their characteristics. The current status of the sardine and anchovy resources off California, already mentioned, offers a good example. For years, scientists and others have argued whether the declining sardine resource was a result of overfishing or of natural causes. The present hypothesis is that heavy fishing pressure on sardines when recruitment was seriously reduced by natural causes drove the stock down and allowed the anchovy to increase to fill the void. This was possible because the anchovy resource had been protected by stringent limitations on commercial fishing. As supporting data we have estimates of the abundance of larvae of the two species over a period of about 15 years (Ahlstrom, 1966), continuing poor commercial catches of sardines, and observations on increased abundance of adult anchovies. But whether anchovies became abundant because sardines were scarce, or whether the anchovy found oceanographic conditions particularly favorable to compete with the sardine and so drove the sardine stocks down, no one knows. Evidence suggesting that the California sardine resource has experienced several wide fluctuations in abundance in the past 600 years, whereas anchovy abundance has remained relatively steady until recently, has been put forward by Isaacs (1966).

Recently the California Fish and Game Commission approved a controlled experimental fishery on anchovies which the scientists believe may answer some of these questions. The experimental approach to the question of how fishing affects a stock of fish is intriguing to scientists and managers because it offers the most direct and speedy method for obtaining quantitative measures of the variables under study. Yet this is the first such study to be carried out in United States marine waters. To be successful, such an investigation must be accompanied by carefully planned statistical and biological investigations and must be free from whimsical political interference. Success also hangs on the validity of the assumption that other variables not under study will have negligible effects on the experiment. This is one of the gambles that must be taken when the natural environment is used as a laboratory for experimental studies. It is one thing to carry out a controlled laboratory experiment as Silliman and Gutsell (1962) did, which proved that in the absence of other sources of variation the theory of fishing is valid. It is quite another thing to carry out similar (indeed, more sophisticated) experiments in nature, where many variables must go uncontrolled. From the experimental scientist's point of view this approach might be considered naive. Yet these are the conditions under which fishery management must be conducted. If management of marine resources is to be successful it must be conducted in just such pragmatic terms and not under the unrealistic assumption that rigid control is being exerted. Until we learn to tame nature we must live with her vagaries. This approach has succeeded very well in agriculture.

Of course, controlled laboratory experiment also is an important aid to fishery management. Laboratory studies are essential for testing the general hypotheses upon which management is based, as Silliman and Gutsell (1962) demonstrated so nicely, and for understanding behavior of marine animals. A wide variety of such basic studies is being continued and extended in the Fish and Wildlife Service and in State and private laboratories. One of the principal faults of fishery science in the past has been to concentrate too much on narrow studies of single species or stocks. This approach may be satisfactory for a few species or fisheries but not for many (McHugh, 1959). Although we have made great progress in fishery science in America in the last half century it is a hard fact that very few of our fisheries are now under effective management to maintain or to increase the maximum sustainable yield. To husband our estuarine fishery resources we will need to understand the biology and ecology of species and populations a great deal better than we now do.

The examples used have been taken mostly from high-seas marine fisheries. It was stated previously that in no estuarine fishery has the relation between fishing effort and maximum sustainable yield been demonstrated as clearly as it has in some oceanic fisheries. This might be challenged by managers of oyster and Pacific salmon resources, but they cannot deny that natural and human forces other than fishing complicate the management of such estuarine fisheries. We should manage these fisheries on the basis of the best information at hand, recognizing that the outcome will not always be exactly as it was expected, rather than to throw up our hands and say that nothing can be done because our knowledge is incomplete. To understand and control the population dynamics of estuarine fishery resources, living as they do in a highly variable and in some respects hostile environment, beset by the mounting effects of technological development, will require much more than a simple understanding of the effects of fishing. Management of most estuarine fisheries is a much more difficult task than management of a fishery which conforms to a hypothetical and relatively simple model. This is why management of estuarine fisheries generally lags behind management of some of our marine fisheries.

Administrative Aspects

Effect of social developments.—Sanford (1965) has made the trenchant point that specialization in inquiry and teaching, although it has played a necessary and very effective role in recent development of our society, has created serious social problems and has led to a neglect of the generalist approach in science. He says: "The potentiality for creating fresh human problems is inherent in the dynamics of specialized knowledge, whose sudden thrusts within a limited sector of a social system create imbalances in the whole." As an example, he cites the great advances in medical science which have come from specialized scientific inquiry, yet have produced an unprecendented human "population explosion" which has catastrophic implications for mankind.

This rapid increase in human population, coupled with the technological revolution which has been created by scientific specialization, has vastly increased the complexity of estuarine fishery problems. The "population explosion" has been accompanied by parallel increases in the effects of human population on the estuarine environment, such as domestic and industrial pollution and engineering developments. The technological revolution has brought about increased prosperity and leisure time which have led to increased recreational uses of the estuarine zone. It has also introduced new factors, such as detergents, pesticides, radioactivity, and other chemical and physical influences, most of which are likely to interfere with, rather than to heighten, our enjoyment of the estuarine environment and our utilization of its resources. Our knowledge of the ecology of estuaries and the responses of their living resources to these new stresses has not kept pace with these developments. The social and political mechanisms for dealing with this growing complex of problems have advanced scarcely at all in the last 100 years. As Sanford (1965) has so aptly pointed out, with respect to quite another set of problems: "The apparatus originally set up for coping with particular problems, having generated momentum and built into itself self-perpetuating mechanisms, continues to operate along the same lines as before."

Nowhere is the contrast between scientific and technological advancement and administrative conservatism illustrated better than in the sphere of estuarine fishery management in the United States. Many State and local laws hinder rather than stimulate development and wise use of fishery resources, yet many of these laws were passed with these commendable purposes in mind. Other laws, policies, and administrative actions have had less noble motives, aimed at creating vested interests and stifling competition, or at diverting political pressures. Actions designed to prohibit or limit operation of "destructive" types of gear, and creation of study groups or commisions to consider a problem, are examples of such moves. Creation of a special permanent or self-liquidating agency or body to deal with difficult problems is a particularly useful device, whether the purpose be altruistic or selfish. Although creation of a study group is not always a popular solution to a fishery problem, it often is the most appropriate action. The short-term effect can be to ease political pressures very effectively. If the group is properly supported and staffed, its long-term effect will be to improve scientific and public understanding of the problem. Too often, however, the agency is forced to assume the problems without the tools to deal with them effectively. Although the situation is improving slowly, the quality of research and management still is hampered seriously by inadequate financial support and facilities, and in some cases by low salaries. The legislature which created the agency may be unable or unwilling to support it adequately for various reasons. Consequently, performance may be inadequate and poor, the caliber of personnel is apt to deteriorate, and the public transfers its criticism from the lawmakers to the agency, often abetted by the very people who created the agency in the first place. Even if support is adequate and personnel are competent, the odds may be heavily against strong public acceptance and support of scientific fishery research and management unless the research has been underway long before a particular problem arises. If the basic knowledge needed to solve a problem is not available when a problem appears, it may be quite inappropriate to respond to the stimulus by attacking the problem too narrowly. This can lead to a series of unrelated investigations, each one too narrow and too late.

Sanford (1965) has made a number of pertinent comments on the need for such a broad approach. He says:

> "Knowledge of how things cling together is at least as important a part of science as is knowledge of how things may be analyzed.
>
> "This last is freely admitted by most scientists, but the objection is often made that complex wholes and wide ranges of variables cannot be studied by existing scientific methods. The answer is that we *must*, sooner or later, study complex and wide-ranging phenomena if our sciences are ever to become fully developed. . . . In thinking comprehensively and holistically about human and social problems, the scientist must use gross units of analysis; and he must content himself with rough estimates of the variables he studies. He cannot hope to achieve the refinement of conceptualization and the precision of measurement that is achieved by the laboratory man, but this does not make him any the less scientific. . . ."

These remarks apply very nicely to fishery science, which is just as much a social as it is a natural science. The distinction that most natural scientists make between their own field of specialization and the social sciences is a puzzling one, for the only real distinction is that the social sciences relate to people, whereas the so-called natural sciences do not. Presumably all inquiry, no matter what the semantic connotations are, has some value to people. Thus, estuarine fishery research and management, like fishery sicence and management in general, is the broadest kind of ecology (McHugh, 1962), for it cannot be brought to full development unless it gives due weight to human social behavior.

Types of fishery regulation.—Fishery regulations in common use in estuarine waters fall into three principal classes, which apply to the fish, to the gear, or to the fishing operation. Laws applying to the resource include minimum (and sometimes maximum) size limits, bag limits or quotas, and limitations on the kinds of fish that may be caught or retained. Gear restrictions concern such things as the dimensions of nets, mesh size, and number of units of gear per fisherman or vessel. Limitations on fishing operations are various, and include closed seasons, closed areas, specification of sites for fixed gears, and many rules on the way in which gear must be used. The laws of most coastal States contain innumerable variations of these methods of restriction, some designed to eliminate conflicts or to provide for safe navigation, but many with conservation as their stated objective. The management value of most of these regulations has not been tested and it is probable that these laws as a whole increase the cost of catching fish but have little effect in maintaining or increasing the supply. Some States have recognized the need to improve their fishery laws and have made substantial revisions, but much more revision and public education is necessary.

Economists who have studied fishery management schemes are invariably puzzled by the emphasis on regulating fishing methods without limiting total fishing effort (Scott, 1962; Sinclair, 1962). When sufficient information is available to establish a catch quota to maintain the maximum sustainable yield, and this quota can be enforced, the resource is protected but the economic position of the industry is not. It has been pointed out many times that if entry of gear into the fishery is not also limited in such a way as to maintain the maximum economic yield, the number of units of effort will tend to come into equilibrium at a level that just balances the cost of catching fish. A recent study of the salmon fishery in northern waters of the State of Washington (Royce et al., 1963) showed that the research of the International Pacific Salmon Fisheries Commission, although it has made great progress in rehabilitating the salmon runs of the Fraser River, has not improved the economic position of the individual fishermen. The increased catch is simply shared by a larger number of fishermen, and this increase has endangered the conservation program. It was estimated that the same catch could be made by reducing the number of fishermen by one third.

If all operators do not follow good business practices by reserving capital to replace vessels and gear, the fishermen will earn low wages on the average and eventually will be in serious financial difficulty. This problem is particularly acute in many segments of the estuarine fisheries, where capital investment by the individual fisherman is relatively modest and business acumen is not strongly developed. When the characteristically wide variation in abundance of living estuarine resources is superimposed upon an industry philosophically geared to a steady state condition, even the largest and most efficient operators may be in trouble, for the common property nature of fishery resources not only tends to attract more capital investment than is necessary to harvest and process the resource most efficiently, but also tends to over invest capital in order to handle peak, rather than average, production. This often leads to the mistaken notion that scientific management can maintain peak production, a concept which ignores the principles of ecology.

Estuarine fisheries are difficult to manage by conventional methods because many types of gear capture a variety of species and most species are harvested at different times and different places by several kinds of gear. This subject was discussed rather thoroughly before an earlier meeting of the American Fisheries Society (McHugh, 1959). The growing sport-fisheries further complicate the problem because many are unregulated and not well understood and because the basic interests of recreational and commercial fishermen are so different.

Interactions between sport and commercial fisheries.—Controversies between recreational and commercial fishermen are growing year by year as the human population grows and enjoys more leisure time. Many arguments are raised by both sides, some thoughtful, some emotional, and the problem has been complicated by hasty actions and statements by sportsmen, commercial fishermen, scientists, and administrators. The essential problem is to understand the issues, biological and social, to educate all parties, to maintain the resources at their optimum productive levels, and to decide how the catch shall be shared. The final decision must be made on social-political grounds; but if it is to be made wisely, our understanding of the biological background must be improved. Whatever the decision, to reserve some resources for recreation, to set aside others for commercial use, and to mark others for joint use as now prevails, it will be necessary to improve our knowledge of the biology of the species and their environments and to gather adequate statistics on catch and effort. Good biological statistics for this purpose are not available for all commercial fishery resources, but the state of our knowledge of catch and fishing effort in the commercial fisheries is far ahead of our knowledge of the estuarine sport fisheries, for which we have only fragmentary order-of-magnitude knowledge. If the interests of sport fishermen are to be protected they must assume responsibility for cooperation in providing the necessary data. In the long run, unregulated sport fishing, like unregulated commercial fishing, will work against the interests of all fishermen.

One important aspect of the relationship between sport and commercial fishing has received little attention. The interests of the sport fisherman, if they lie principally in matching his skills against those of this quarry, will be served best if the resource is at maximum abundance. For this purpose he might improve his chances of getting strikes by returning his catch to the water unharmed, as some sport fishermen do. The commercial fishermen, on the other hand, usually aim to harvest the maximum sustainable yield. This will reduce the abundance of the resource, but it is not overfishing. If the resultant level of population size happens to be 50 percent of the magnitude of the virgin stock, the commercial fisherman will be enjoying maximum use of the resource. On the contrary, the sport fisherman seeking the same resource will find that his catch per unit of effort is only half of what it was at some time in the past, and that there are fewer large fish in his catch. Naturally, he will blame the commercial fisherman. Such anomalous situations are among the factors causing misunderstandings between the two groups. If sport and commercial fishermen are sharing a resource, this problem will be insoluble if neither side is willing to compromise.

Of course, not many sport fishermen return their catch to the water. They retain their fish for various reasons, to demonstrate their skill, to enjoy fresh fish, or to sell in the market. A substantial part of the so-called sport catch of some species, such as Pacific salmon, Atlantic bluefish, and a number of semi-tropical species in the Gulf of Mexico, end up in commercial markets. The philosophy of most sport fishermen is that the individual catch is negligible, hence has insignificant effects upon the resource. It is only when general estimates of the total sport catch are made (Anonymous, 1962; Frisbie and Ritchie, 1963; Harmic, 1956; Miller and Gotshall, 1965; Richards, 1962; Younger and Zamos, 1955) that the magnitude of the recreational fishery for some species becomes evident. The sport catch of some estuarine fishes is substantial, rivalling or exceeding the commercial catch of some species in some areas. This demands recognition by all fishermen of a responsibility to cooperate in providing the information necessary for management and to support the scientific programs of the States and the Federal Government.

As the estuarine sport fisheries grow there are increasing pressures on State legislatures to restrict commercial fishing activities on the grounds that they are interfering in various ways with recreational fishing. These proposals take two principal forms, prohibitions on fishing by certain kinds of gear in certain areas, or complete bans on commercial fishing for certain species. There is little scientific basis for most of these arguments, although many of them are supported by pseudo-ecological rationalization. Usually it is easy to develop equally plausible arguments in rebuttal. The natural human tendency to oversimplify the complicated relationships between natural and man-made forces, especially in the absence of definitive knowledge, makes it easy to develop a convincing case for a particular point of view. There is also a general lack of public understanding of the methods and objectives of commercial fishing, as exemplified by the growing opposition to menhaden purse-seining in some areas, and a tendency to exaggerate the potential effects of commercial fishing on the sportsman's hobby. Hostility is fostered by the actions of some commercial fishermen, who thoughtlessly or deliberately flout public opinion. The menhaden industry has seen the need for leadership and has drawn up a code of ethics for itself, with severe penalties for industry members who fail to comply. In some areas menhaden fishermen and sport fishermen are cooperating in various ways, to mutual benefit.

There is nothing in the controversies between commercial and recreational fishermen that cannot be resolved by tolerance and understanding and a mutual desire to negotiate. Perhaps the principal need, other than the urgent need for better scientific knowledge, is for a suitable forum in which the issues can be debated coolly and rationally and a basis of understanding reached. The only means available at present are the press or the trade magazines, where the arguments are stimulated rather than resolved, or before State legislative committees. In the absence of adequate knowledge, legislative action seldom arrives at the most equitable solution and may do great injustice. It is time that these two groups resolved their differences in order to unite against the real threat, the diverse changes in the estuaries caused deliberately or inadvertently by man's increasing numbers and technological development.

SUMMARY AND CONCLUSIONS

Fringing the North American continent are some of the most extensive estuarine systems in the world. This is especially true if it is recognized that large areas of the ocean adjacent to our coasts are affected substantially by land drainage. The definition of an estuary which places an arbitrary seaward boundary based on features of the land is too restrictive a definition to be very useful to the fishery scientist. The ecology of estuarine fishery resources is best understood by recognizing that the estuary extends out to sea.

A large part of the United States fish catch is based on species which appear to be estuarine dependent. Most of these fisheries do not conform nicely to the models underlying fishery management because estuarine resources are subject to wide variations in abundance from natural causes, and from a variety of fishery-independent causes of human origin. The complex of forces acting on estuarine fishery resources, and the variety of conflicting interests involved, introduce strong social-political complications. The scientific facts necessary as a basis for management of estuarine fisheries are largely lacking because scientific research has not been supported adequately. Even when the necessary scientific knowledge exists, it is often impossible to apply this knowledge effectively because local traditions and laws prevent it. This is why none of our estuarine fishery resources is under successful management in the sense that North Pacific halibut and Bering Sea fur seals are under management. This is why management models are not available for any estuarine fishery in the sense that such models are available for yellowfin tuna in the eastern tropical Pacific or for baleen whales in the Antarctic. Growing foreign fisheries off our shores are adding further complications.

Management of estuarine fisheries, if they are to be managed at all, will require very broad and basic ecological research, much more sophisticated and intense than any research now underway. The important and complicated role played by man must not be ignored, and this will require the attention of economists, sociologists, political scientists, psychologists, legal experts, and engineers, among others. Finally, ways must be developed to improve public understanding of the issues involved and to provide equitable means of resolving incompatible interests. The problem calls for understanding and statesmanship of an order heretofore never realized. The task is extremely difficult and the best routes to follow are not always clear. The rewards will be preservation of important commercial and recreational resources, development of other resources now being ignored, and techniques for improving on nature and increasing the yields of useful products from the sea.

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ORGANIZATION AND ADMINISTRATION OF FISHERY RESEARCH IN THE UNITED STATES OF AMERICA

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Abstract

The responsibilities for fisheries research in the United States are shared by a variety of Federal, State and other governmental and non-governmental organizations. Generally, the Federal Government conducts fishery research of broad scope, related to resources common to waters of several States or inhabiting international waters. Scale and organization of fishery research in States differ from one to another. In several cases, Interstate fisheries commissions carry out their fishery research. A number of universities are engaged in fishery research and training of fishery scientists. A part of the activities is supported by Federal and State Governments and the fishing

industry. In view of the variety of organizations engaged in fishery research, a number of consultative machineries have developed with the government as well as between governmental and non-governmental institutions. National objectives of research are supported and directed by the Fish and Wildlife Act of 1956 and other statutory authorities, actions of the Congress, and recommendations by interstate fishery commissions. The paper deals in detail with the institutional framework of research, consultative arrangements, process of formulation of research objectives, planning and conduct of research, and reporting and application of research results.

ORGANISATION ET ADMINISTRATION DE LA RECHERCHE HALIEUTIQUE AUX ETATS-UNIS D'AMERIQUE

Résumé

Aux Etats-Unis d'Amérique, la recherche halieutique incombe à un certain nombre d'organismes fédéraux, des Etats, ou autres institutions gouvernementales ou non gouvernementales. C'est en général le Gouvernement Fédéral qui dirige les travaux de recherche halieutique d'une grande portée, touchant des ressources communes aux eaux de plusieurs Etats ou habitant des eaux internationales. L'importance et l'organisation de la recherche halieutique à l'échelon des Etats varie de l'un à l'autre. Dans plusieurs cas, la recherche relève de commissions interétatiques des pêches. Plusieurs universités s'occupent de recherche halieutique et de la formation de spécialistes dans ce domaine. L'activité bénéficie en partie du soutien du Gouvernement fédéral, des Gouvernements des Etats, et de l'industrie des pêches. Etant donné la variété des organismes s'occupant de recherche halieutique, divers dispositifs consultatifs ont été créés tant au sein du gouvernement qu'entre institutions gouvernementales ou non gouvernementales. La recherche visant des objectifs d'intérêt national est financée et dirigée conformément au Fish and Wildlife Act (Loi relative aux pêches et à la faune sauvage) de 1956, et s'exerce aussi conformément aux décisions d'autres organisms statutaires ou du Congrès, et aux recommandations des commissions interétatiques des pêches. La communication expose de façon circonstanciée la structure institutionnelle de la recherche, les dispositions d'ordre consultatif, la manière dont sont formulés les objectifs de la recherche, l'organisation et l'exécution de celle-ci, et la publication et l'application de ses résultats.

ORGANIZACION Y ADMINISTRACION DE LAS INVESTIGACIONES PESQUERAS EN LOS ESTADOS UNIDOS DE AMERICA

Extracto

Las responsabilidades de la investigación pesquera en los Estados Unidos las comparten una variedad de organizaciones federales, estatales, y de otras gubernamentales y no gubernamentales. En general, el Gobierno Federal realiza investigaciones pesqueras de amplio alcance, relativas a los recursos comunes a las aguas de los distintos Estados o a las aguas internacionales. La escala y organización de las investigaciones pesqueras en los Estados varía de uno a otro. En varios casos, las comisiones pesqueras interestatales realizan sus propias investigaciones pesqueras. Algunas universidades se ocupan de las investigaciones pesqueras así como de la capacitación de especialistas en pesca. Una parte de las actividades la respaldan el Gobierno Federal y los de los Estados y la industria pesquera. Teniendo en cuenta la variedad de organizaciones que se ocupan de las investigaciones pesqueras, se han creado dentro del Gobierno, así como entre las instituciones gubernamentales y no gubernamentales, algunos organismos consultivos. La Ley de 1956 de pesca y vida silvestre, y otras leyes oficiales, medidas del Congreso, y recomendaciones de comisiones pesqueras interestatales, apoyan y dirigen los objetivos nacionales de investigación. El estudio se ocupa detalladamente de la estructura institucional de la investigación, medidas consultivas, procesos de formulación de los objetivos de las investigaciones, preparación y realización de éstas, e información y aplicación de los resultados de la investigación.

TABLE 1. LANDED VALUE OF UNITED STATES CATCH BY STATES IN 1962 OF ALL KINDS OF FISHERY PRODUCTS FOR WHICH THE TOTAL LANDED VALUE WAS $1.0 MILLION OR GREATER. THE EIGHT STATES NOT LISTED HAD NO COMMERCIAL FISHERIES.

States	Total Value and Weight		Rank by value in total United States landings:											
	Thousands of dollars	Thousands of pounds	1 Shrimp	2 Salmon	3 Tuna	4 Oysters	5 Menhaden	6 Crabs	7 Lobsters	8 Flounders	9 Scallops	10 Clams	11 Halibut	12 Hadde
1. Alaska	57,242	429,218	732	42,119	0	0	0	6,281	0	0	0	79	7,467	
2. California	54,969	518,020	198	4,023	41,082	307	0	889	354	1,578	0	2	1	
3. Massachusetts	40,265	493,414	6	+	442	81	139	6	2,196	7,360	8,912	1,125	48	10,7
4. Florida	32,353	197,823	17,099	0	0	1,427	322	1,157	1,188	64	73	51	0	
5. Louisiana	30,333	776,621	16,985	0	0	3,317	7,996	635	0	33	0	0	0	
6. Texas	30,231	172,516	27,149	0	0	473	1,137	290	0	31	0	0	0	
7. Virginia	21,701	453,901	0	0	+	9,774	3,884	2,952	10	385	33	813	0	
8. Maine	20,365	294,323	51	+	12	1	0	68	11,196	85	876	895	30	1
9. Washington	18,939	117,584	136	7,642	65	2,193	0	1,060	0	935	0	266	4,010	
10. Maryland	11,926	67,574	0	0	+	6,182	77	2,368	1	158	0	1,697	0	
11. New Jersey	11,824	446,929	7	0	1	1,423	3,902	172	369	983	166	2,460	0	
12. New York	10,309	226,439	0	0	3	1,079	1,263	0	163	766	1,819	3,033	0	
13. Mississippi	8,378	373,522	2,220	0	4	537	2,917	35	0	7	0	0	0	
14. Oregon	7,839	61,005	273	2,369	1,497	128	0	1,127	0	981	0	18	101	
15. North Carolina	6,755	182,384	2,239	0	0	485	1,364	528	0	227	67	99	0	
16. South Carolina	4,720	22,680	2,813	0	0	1,160	0	293	0	27	0	20	0	
17. Georgia	4,553	22,136	3,800	0	0	51	0	437	14	3	0	0	0	
18. Rhode Island	3,528	76,830	0	0	85	8	64	20	321	636	6	953	0	
19. Alabama	3,335	16,969	1,647	0	0	164	0	35	0	12	0	0	0	
20. Delaware	3,106	271,606	0	0	0	60	2,783	128	0	5	0	155	0	
21. Hawaii	2,820	13,157	1	0	1,921	0	0	24	5	0	0	2	0	
22. Michigan	2,479	22,131	0	0	0	0	0	0	0	0	0	0	0	
23. Wisconsin	1,886	29,447	0	0	0	0	0	0	0	0	0	0	0	
24. Connecticut	1,216	6,026	0	0	0	381	+	1	366	96	144	94	0	
25. Ohio	1,139	13,223	0	0	0	0	0	0	0	0	0	0	0	
26. Tennessee	797	7,575	0	0	0	0	0	0	0	0	0	0	0	
27. Minnesota	786	14,065	0	0	0	0	0	0	0	0	0	0	0	
28. Illinois	613	6,653	0	0	0	0	0	0	0	0	0	0	0	
29. Arkansas	613	5,277	0	0	0	0	0	0	0	0	0	0	0	
30. New Hampshire	401	1,089	0	0	0	0	0	2	355	0	0	0	1	
31. Kentucky	294	2,555	0	0	0	0	0	0	0	0	0	0	0	
32. Iowa	176	2,326	0	0	0	0	0	0	0	0	0	0	0	
33. Pennsylvania	130	2,130	0	0	0	0	0	0	0	0	0	0	0	
34. South Dakota	116	2,716	0	0	0	0	0	0	0	0	0	0	0	
35. Oklahoma	57	426	0	0	0	0	0	0	0	0	0	0	0	
36. Nebraska	35	308	0	0	0	0	0	0	0	0	0	0	0	
37. Missouri	35	287	0	0	0	0	0	0	0	0	0	0	0	
38. Indiana	30	634	0	0	0	0	0	0	0	0	0	0	0	
39. North Dakota	27	343	0	0	0	0	0	0	0	0	0	0	0	
40. Montana	9	86	0	0	0	0	0	0	0	0	0	0	0	
41. Kansas	8	32	0	0	0	0	0	0	0	0	0	0	0	
42. Wyoming	5	174	0	0	0	0	0	0	0	0	0	0	0	
GRAND TOTALS	396,420	5,354,183	73,236	56,353	45,112	29,139	25,866	18,708	16,314	14,390	12,096	11,762	11,658	10,

IN THOUSANDS OF DOLLARS. THESE 31 KINDS OF FISH MADE UP OVER 94 PERCENT OF THE TOTAL LANDED VALUE OF ALL UNITED STATES COMMERCIAL FISHERIES IN 1962.

14 Catfish & Bullheads	15 Snappers	16 Cod	17 Sea Herring	18 Scup	19 Mullet	20 Whiting	21 Jack Mackerel	22 Buffalo-fish	23 Chubs	24 Sea Trout	25 Sea Bass	26 Shad	27 Mackerel	28 Striped Bass	29 Yellow Perch	30 Carp	31 Butterfi
0	0	0	379	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	49	0	0	0	1,869	0	0	0	150	0	1,027	0	0	11	0
0	0	2,760	40	67	0	1,656	0	0	0	0	6	1	229	85	0	0	118
1,972	1,864	0	0	5	2,013	0	0	0	0	815	5	81	0	0	0	0	0
1,808	157	0	0	0	+	0	0	420	0	78	0	0	0	0	0	11	0
46	444	0	0	0	2	0	0	39	0	249	0	0	0	0	0	1	0
162	0	4	0	763	9	18	0	0	0	165	667	312	29	279	3	10	138
0	0	107	2,375	0	0	274	0	0	0	0	0	+	3	0	0	0	+
0	0	150	156	0	0	0	0	0	0	0	0	39	0	0	0	13	0
20	0	42	+	5	+	4	0	0	0	9	29	395	2	642	13	10	6
2	0	175	4	996	2	157	0	0	0	59	342	73	5	91	0	6	142
16	0	113	1	763	0	122	0	+	0	9	102	33	18	96	30	1	151
138	544	0	0	0	26	0	0	225	0	33	0	0	0	0	0	22	0
0	0	1	7	0	0	0	0	0	0	0	+	175	0	6	0	0	0
85	1	0	0	23	161	0	0	0	0	211	147	191	5	120	3	4	16
32	4	0	0	1	223	0	0	0	0	6	43	32	0	0	0	+	0
18	+	0	0	0	+	0	0	0	0	+	+	132	0	+	0	+	0
0	0	60	5	402	0	96	0	0	0	1	22	1	26	10	0	0	403
306	495	0	0	0	71	0	0	67	0	13	0	0	0	0	0	16	0
0	0	4	0	+	1	0	0	0	0	16	0	15	0	11	0	1	+
0	159	0	0	0	42	0	124	0	0	0	10	0	0	0	0	0	0
60	0	0	0	0	0	0	0	+	994	0	0	0	0	0	173	126	0
113	0	0	0	0	0	0	0	148	696	0	0	0	0	0	279	303	0
0	0	25	1	65	0	15	0	0	0	1	5	81	1	5	0	1	10
247	0	0	0	0	0	0	0	3	0	0	0	0	0	0	404	105	0
308	0	0	0	0	0	0	0	142	0	0	0	0	0	0	0	85	0
109	0	0	0	0	0	0	0	53	0	0	0	0	0	0	37	150	0
193	0	0	0	0	0	0	0	191	16	0	0	0	0	0	22	124	0
175	0	0	0	0	0	0	0	360	0	0	0	0	0	0	0	28	0
0	0	4	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
160	0	0	0	0	0	0	0	60	0	0	0	0	0	0	0	22	0
65	0	0	0	0	0	0	0	37	0	0	0	0	0	0	0	36	0
+	0	0	0	0	0	0	0	0	0	0	0	0	0	0	144	+	0
7	0	0	0	0	0	0	0	88	0	0	0	0	0	0	0	11	0
16	0	0	0	0	0	0	0	29	0	0	0	0	0	0	0	4	0
13	0	0	0	0	0	0	0	2	0	0	0	0	0	0	+	20	0
13	0	0	0	0	0	0	0	12	0	0	0	0	0	0	0	6	0
3	0	0	0	0	0	0	0	1	0	0	0	0	0	0	+	+	0
11	0	0	0	0	0	0	0	11	0	0	0	0	0	0	+	3	0
5	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	+	0
2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	5	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0
6,176	3,648	3,453	3,117	3,048	2,551	2,340	1,993	1,913	1,706	1,670	1,628	1,367	1,346	1,345	1,105	1,046	1,003

ORGANIZATION AND ADMINISTRATION OF FISHERY RESEARCH IN THE UNITED STATES OF AMERICA

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1. Introduction

People in the United States are highly selective in their fish-eating habits. If we define kinds of fish broadly, so that the generic term salmon includes all species of *Oncorhynchus* and *Salmo*, the term clams includes all bivalve mollusks other than oysters, mussels, and scallops, and so on, then the 12 most important kinds of fish in our domestic landings make up more than 82 percent of the total landed value. These 12, in order of importance by value, are shrimp, salmon, tuna, oysters, menhaden, crabs, lobsters, flounders, scallops, clams, halibut, and haddock. Menhaden are not consumed directly by man, but menhaden meal and solubles are important constituents of the diet of much of the poultry consumed by Americans.

Locally, there is some variation in the kinds of fish that dominate commercial catches (Table 1). For example, salmon dominate landings in Alaska, tuna in California, lobsters in Maine, menhaden in Delaware, oysters in Virginia, and shrimp in Texas. But in any particular region of the United States the bulk and value of commercial landings are made up of but a few kinds of animals. Almost every coastal State also has underutilized or latent resources off its shores.

The outstanding feature of the United States domestic fishery is that the major and most desirable species are probably producing close to the maximum sustainable yield. Some, indeed, have been exploited beyond this point and research programs are attempting to produce information needed to restore the maximum productivity. Our tuna and shrimp fleets have acted to supply the increasing demand for these species by extending their operations into distant waters, but the United States has no counterpart of the large fleets of motherships and catcherboats with which other nations have pushed their fisheries into all parts of the world ocean. Per capita consumption of fish in the United States has remained fairly steady, and to maintain this rate of consumption we have been importing an increasingly large amount of fish. In 1963, for the first time, imports of edible fish into the United States exceeded domestic production. These imports consisted almost entirely of fish meal, oil, and solubles, or of the 12 most valuable and desirable kinds of fish in the United States domestic catch (Table 2). The other important components of imports were fish meal, oil, and solubles.

The Constitution of the United States delegates to the Federal Government a few well-defined powers and leaves to the individual States numerous indefinite responsibilities. Among the powers that the Constitution delegates to the States by implication is the responsibility to manage their respective fisheries and presumably to conduct the necessary research. Generally, the States defend vigorously their right to manage their fishery resources, but individually they vary widely in their ability to do so. Many of our major marine fishery resources migrate freely from the waters of one State to another, or at least include the waters of several States within their geographic range, so that they are exploited by the fishermen of several States and should be managed jointly. Recognizing the need for joint consideration of fishery problems the maritime States have executed compacts for the purpose, one on the Pacific coast, one on the Atlantic, and one on the Gulf of Mexico (Appendix I). Two of these interstate fishery commissions have designated the Federal Government as their primary research agency.

TABLE 2. PRINCIPAL KINDS OF FISHERY PRODUCTS IMPORTED INTO THE UNITED STATES IN 1963

	Pounds
Fish meal, oil, and solubles	779,760,000
Tuna	300,384,000
Groundfish and ocean perch	231,728,000
Shrimp	151,530,000
Fillets (other than groundfish and ocean perch)	68,488,000
Sperm whale oil	67,328,000
Lobsters	58,538,000
Sardines	41,547,000
Halibut	27,539,000
Scallops	13,343,000
Salmon	10,127,000
Oysters	8,254,000
Bonito and yellowtail	5,865,000
Crabs	5,295,000

Fishery research in the Federal Government is conducted primarily by the Fish and Wildlife Service (FWS) of the Department of the Interior. Research responsibilities are laid down in a variety of statutes, the latest and most comprehensive of which is the Fish and Wildlife Act of 1956 (Appendix II) 1/. Research policy for commercial fisheries is stated and described in "Operation Trident", the long-range program of the Bureau of Commercial Fisheries (BCF) 2/. Research policy for sport fishery resources is described in a similar, but as yet unpublished, long-range program of the Bureau of Sport Fisheries and Wildlife (BSFW). Where the United States exploits fishery resources jointly with other nations, conservation of these resources, management of the fisheries, and the necessary research programs are governed by international conventions and implementing federal legislation. The individual States also co-operate closely in the research and management programs of the international commissions in an advisory capacity, and also conduct some of the research.

1/ U.S. Department of the Interior, Bureau of Commercial Fisheries, Fishery Leaflet No. 557, Sept. 1963.

2/ U.S. Department of the Interior, Bureau of Commercial Fisheries, Circular No. 142, April 1962.

The commercial fishing industry of the United States is not highly organized. There are several important industry and fishermen's organizations, and these together include in their membership most of the important fish processors and many of the primary producers [3]. Individually, however, none of these is uniformly representative of primary producers and processors as a whole, although some segments of industry have strong representative associations. The interests and policies of some of these organizations conflict strongly with those of others.

Altogether, this diversity of organization and interest makes for difficulty in developing and maintaining balanced programs of research directed at the major problems of the fisheries. Because management of resources in territorial waters is the responsibility of the individual States, or in some cases the county or even the individual town, local traditions and prejudices have an important influence on research and management programs. A discussion of the organization, conduct and application of results of fishery research in the United States would not be complete without mention of the major shortcomings and strengths of our complicated system. Consequently, the descriptive sections of this paper will be amplified by critical comments when appropriate. An interesting review of fishery management in America has been published recently by Richard H. Stroud and others [4].

2. Institutional Framework [5]

2.1 Governmental. As explained already, Federal and State Governments in the United States share the responsibility for fishery research. Generally, the Federal Government conducts scientific programs of broad scope related to resources common to waters of several States or inhabiting international waters. Most States have scientists on the staffs of their fishery agencies. Research policies and support vary widely between States. The 15 Atlantic coastal States forming the membership of the Atlantic States Marine Fisheries Commission (ASMFC), and the 5 States of the Gulf States Marine Fisheries Commission (GSMFC), have named the Fish and Wildlife Service as their primary fishery research agency. All these States also support fishery research with State funds. The Pacific coastal States of Washington, Oregon, and California, the original members of the Pacific Marine Fisheries Commission (PMFC), have traditionally defended their rights to do fishery research and handle their own fishery problems. Consequently, the Fish and Wildlife Service does not have the same intimate statutory association with the PMFC.

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[3] List of Fishery Associations in the United States. U.S. Department of the Interior, Bureau of Commercial Fisheries, Fishery Leaflet No. 254, 13 pp., Revised 1963

List of Fishermen's and Fish Shore Workers' Unions in the United States. U.S. Department of the Interior, Bureau of Commercial Fisheries, Fishery Leaflet No. 293, 8 pp., Revised 1963.

List of Fishery Co-operatives in the United States. U.S. Department of the Interior, Bureau of Commercial Fisheries, Fishery Leaflet No. 545, 15 pp., Revised 1962.

[4] Fish Conservation. In: The Fisherman's Encyclopaedia. The Stackpole Company, Harrisburg, Pa., pp. 329-413, 1964.

[5] A useful listing of organizations and officials concerned with Natural Resources in the United States and Canada is published annually by the National Wildlife Federation, 1412 16th Street, N.W., Washington 6, D.C. This includes Federal and State Government agencies, international, national, and interstate commissions, and private organizations.

Fishery research in the Federal Government is the responsibility of the Fish and Wildlife Service of the Department of the Interior, headed by an Assistant Secretary for Fish and Wildlife (Table 3). Responsibility for fishery research is divided between the two Bureaux of the Service, the Bureau of Commercial Fisheries (Table 4) and the Bureau of Sport Fisheries and Wildlife (Table 5). The activities of the Bureaux receive general supervision from the Office of the Commissioner of Fisheries and Wildlife.

Research in the Bureau of Commercial Fisheries is conducted by 20 Biological Laboratories, 6 Technological Laboratories, 6 Exploratory Fishing and Gear Development Bases, an Economics Laboratory, and a number of field stations. Facilities and programs at these laboratories are described by Hiatt (1963)[6] and McKernan (1963)[7].

Oceanographic research in the United States is carried out or supported by a number of Departments, including Navy; Interior; Commerce; and Health, Education, and Welfare (HEW); and several specialized agencies such as the Smithsonian Institution, National Science Foundation (NSF), and the Atomic Energy Commission (AEC). Co-ordination of the research programs of these agencies is effected through a Committee of the Federal Council for Science and Technology (FCST), the Interagency Committee on Oceanography (ICO). All marine fishery research of the two Bureaux of the Fish and Wildlife Service is reviewed by the President's Office of Science and Technology (OST) through this mechanism (Table 6).

Research on marine sportfish resources is a relatively new activity of the Bureau of Sport Fisheries and Wildlife conducted by two laboratories, one at Sandy Hook, New Jersey, and one at Tiburon, California. Two other such laboratories are planned, one in the State of Rhode Island and one on the Gulf of Mexico coast. Some species of commercial value, such as Pacific salmons and Atlantic scup and weakfishes, are also important sport fishes. Where large research programs of long standing are under way in the Bureau of Commercial Fisheries, such as the extensive investigations of salmon in Alaska and the Pacific Northwest, the Bureau of Sport Fisheries and Wildlife avoids duplication and relies upon its sister Bureau to develop the scientific information needed by both. Conversely, as newer programs of marine sportfish research develop on species of joint interest, such as Atlantic bluefish (Pomatomus saltatrix), the Bureau of Commercial Fisheries will refrain from developing similar studies. The two Bureaux also plan their research in close collaboration with the States, generally avoiding programs of local interest in favour of problems of broad application beyond the capabilities or authority of the individual States.

The Bureau of Sport Fisheries and Wildlife operates 16 research laboratories, major investigations, or programs concerned with sport fishery resources[8]. Most of these are specialized activities, some of them of long standing, dealing with such matters as fish pathology, nutrition, husbandry, control, and effects of pesticides. More recently, investigations of sport fisheries in large reservoirs and in the marine environment have been established. Fishery research by the two Bureaux in reservoirs, as in the sea, is co-ordinated for maximum benefit to sport and commercial fishery interests.

6/ Hiatt, Robert W. 1963. World Directory of Hydrobiological and Fisheries Institutions. Amer. Inst. of Biol. Sciences, Washington, D.C. viii + 320 pp.

7/ McKernan, Donald L. 1963. United States Department of Interior, The Bureau of Commercial Fisheries. American Zoologist, Vol. 3, No. 3, August 1963: 361-386.

8/ Progress in Sport Fishery Research 1963. United States Department of the Interior, Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife, Circular 178: iv + 180 pp.

TABLE 3. ORGANIZATION OF THE UNITED STATES DEPARTMENT OF THE INTERIOR

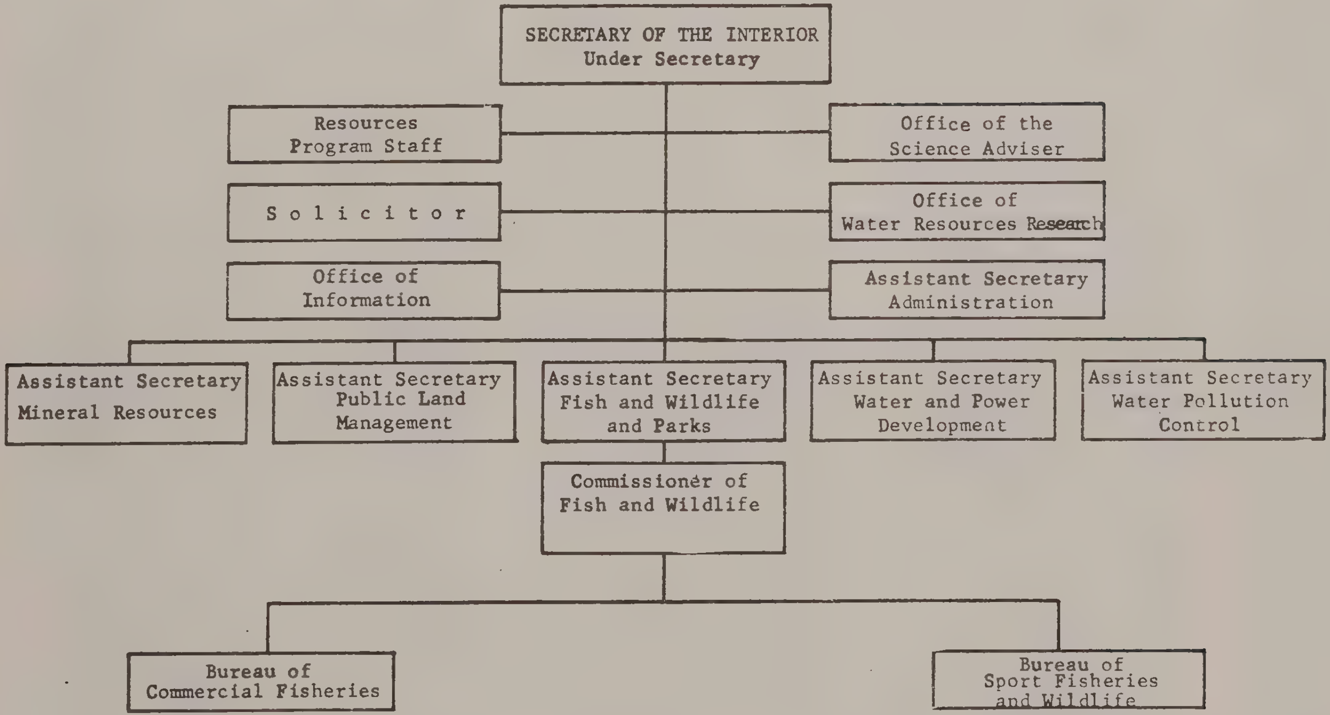
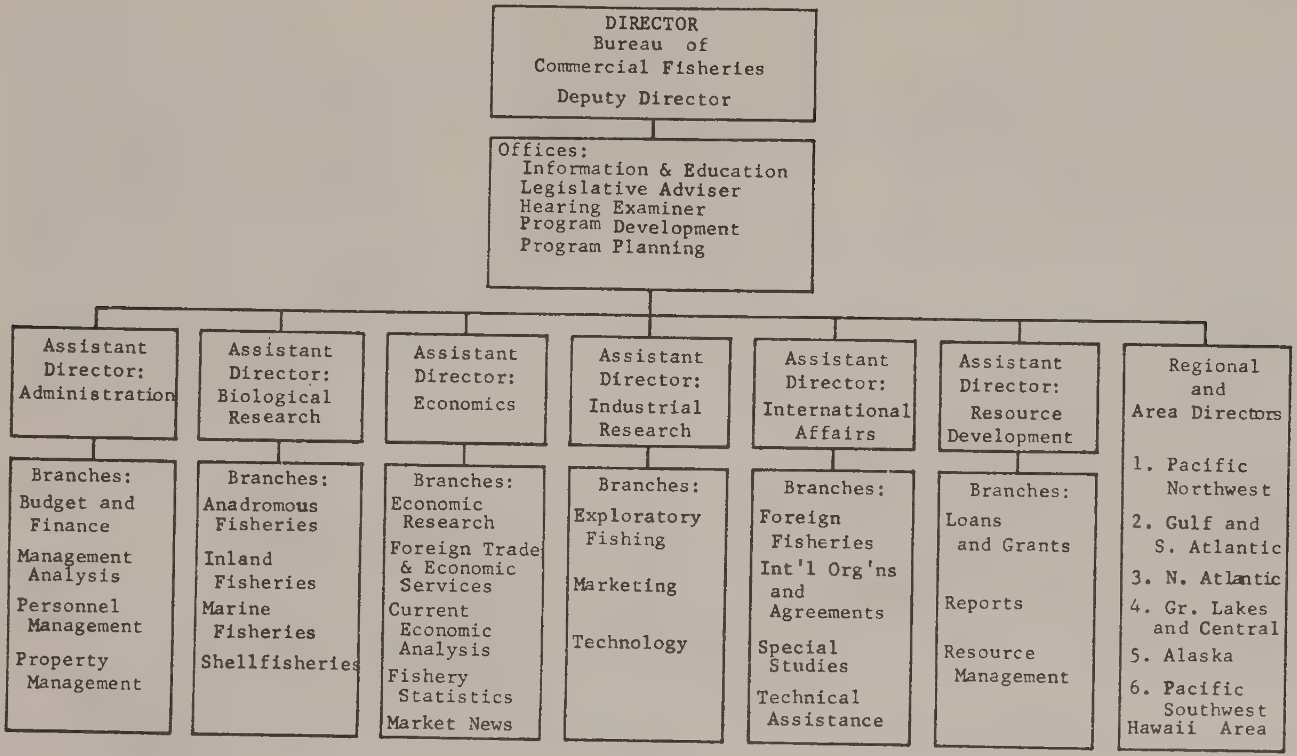

SECRETARY OF THE INTERIOR
Under Secretary
Resources Program Staff
Office of the Science Adviser
Solicitor
Office of Water Resources Research
Office of Information
Assistant Secretary Administration
Assistant Secretary Mineral Resources
Assistant Secretary Public Land Management
Assistant Secretary Fish and Wildlife and Parks
Assistant Secretary Water and Power Development
Assistant Secretary Water Pollution Control
Commissioner of Fish and Wildlife
Bureau of Commercial Fisheries
Bureau of Sport Fisheries and Wildlife

TABLE 4. ORGANIZATION OF THE UNITED STATES BUREAU OF COMMERCIAL FISHERIES


DIRECTOR
Bureau of
Commercial Fisheries
Deputy Director
Offices:
Information & Education
Legislative Adviser
Hearing Examiner
Program Development
Program Planning
Assistant Director: Administration
Branches:
Budget and Finance
Management Analysis
Personnel Management
Property Management
Assistant Director: Biological Research
Branches:
Anadromous Fisheries
Inland Fisheries
Marine Fisheries
Shellfisheries
Assistant Director: Economics
Branches:
Economic Research
Foreign Trade & Economic Services
Current Economic Analysis
Fishery Statistics
Market News
Assistant Director: Industrial Research
Branches:
Exploratory Fishing
Marketing
Technology
Assistant Director: International Affairs
Branches:
Foreign Fisheries
Int'l Org'ns and Agreements
Special Studies
Technical Assistance
Assistant Director: Resource Development
Branches:
Loans and Grants
Reports
Resource Management
Regional and Area Directors
1. Pacific Northwest
2. Gulf and S. Atlantic
3. N. Atlantic
4. Gr. Lakes and Central
5. Alaska
6. Pacific Southwest
Hawaii Area

The Tennessee Valley Authority (TVA), an independent agency of the United States Government, is concerned with development of the natural resources of the Tennessee River basin. Fishery matters are handled in the Fish and Game Branch. The area of interest includes parts of the States of Tennessee, Alabama, Mississippi, and Kentucky.

The Federal Government also participates in various ways in the research programs of nine international fishery commissions 9/. The Departments of State and Interior work co-operatively in these endeavours. The United States share [illegible] funds to support the permanent staffs of the Commissions is provided by the State Department, and one United States Commissioner on each Commission is an Interior employee. Some commissions, like the International Great Lakes Fisheries Commission, the International Commission for the Northwest Atlantic Fisheries, and the International North Pacific Fisheries Commission, do not carry on major research programs, but depend upon the member countries to provide the necessary scientific information. For these Commissions the United States share of the research program is supported by the Bureau of Commercial Fisheries. Others, like the International Halibut and Salmon Commissions, and Inter-American Tropical Tuna Commission, employ scientific staffs to conduct their own research programs.

Organization and support of fishery research in the States vary widely. In the inland States particularly, fishery research usually is the responsibility of a division attached directly to the Office of the Director of Conservation, who usually reports to a Conservation Commission. This is true also in some States fronting on the sea, but many maritime States have elevated their fishery agencies to Departmental or Commission status. Some States separate their marine fishery activities from their game and freshwater fishery agencies, and some have given special status to certain segments of their commercial fisheries. Many shellfish-producing States of the Atlantic coast have accorded such special status to their shellfish resources and at least one State has a Shellfish Commission which is distinct and separate from its Department of Fish and Game.

Some States conduct very large fishery research programs, others have none. Where research does exist, support of marine and freshwater programs often comes from different sources. Marine programs usually are financed by appropriations from the State general fund, freshwater programs often are self-supporting, through special funds provided by fishing or hunting license fees. Support of fishery research by the States also may be provided in the form of contracts, grants, or special funds by various Federal or private agencies. Special support of sport fishery research is provided by the Dingell-Johnson Act 10/, which placed excise taxes on fishing tackle in a special fund for transfer to the States, on a matching basis, according to a formula designed to give equitable distribution. The recently-enacted Public Law 309 of the 88th Congress 11/ and Public Law 304 of the 89th Congress provide for similar assistance to the States for commercial fishery research and services, or on anadromous fisheries, on a matching basis from direct appropriations to the Bureau of Commercial Fisheries. In addition, a number of Federal Departments and specialized agencies contract with certain States for research on specified fishery problems.

9/ McKernan, Donald L. 1960. The role of international commissioners in world fisheries. Proceedings, Gulf and Caribbean Fisheries Institute, 13 Annual Session, Nov. 1960, pages 1-21.

10/ Federal aid in fish restoration. Regulatory Announcement No. 65, March 1962. U.S. Dept. of the Interior, Fish and Wildlife Service, Washington 25, D.C., 22 pp.

11/ Commercial fisheries research and development. Federal Register, Vol. 29, No. 194, Oct. 3, 1964. Title 50 - Wildlife and fisheries, Chap. 2, Subchap. F, Part 253, pp. 13607-13609.

In some States the organizational structure for fishery research and management may change radically when one administration succeeds another. This makes for great instability and usually lowers the calibre of research staffs. Many State personnel systems are too conservative and inflexible for effective management of scientific fishery programs. Consequently, the calibre of professional employees and the quality of research are poor in certain areas. Generally, however, there is a growing understanding of the need for research continuity and quality. Many State fishery research agencies are being insulated against whimsical political interference and strengthened by adoption of more liberal policies. A number of States have appointed scientists at the policy-making level in their fishery commissions or departments, with beneficial results. Some have placed their fishery research activities under boards or commissions with technical membership, or even within universities, quite apart from the fishery enforcement arm of the State Government. Such enlightened policies are certain to be adopted more widely, although improvement cannot always be expected to proceed regularly in all States, and reverses may be expected occasionally.

Individual, unco-ordinated fishery research and management by the States cannot deal effectively with fishery problems of mutual concern. Recognizing this, the coastal States have joined forces in three interstate compacts, as mentioned already. A somewhat similar function is performed for the States and Canadian Provincies that border the Great Lakes by the International Great Lakes Fisheries Commission. The primary purpose of each of these joint efforts is to co-ordinate management of fisheries and to provide the necessary research background.

The Atlantic and Gulf States Marine Fisheries Commissions, which have named the Fish and Wildlife Service as their primary research agency, customarily request the Federal Government to do research on specific problems as the need is recognized. These Commissions also obtain Federal funds for research by enlisting support from their representatives in Congress. All three marine fishery commissions provide a mechanism for co-ordination of research programs of State, university, and Federal Government laboratories. In general, joint planning and co-ordination of fishery research by these commissions has progressed more rapidly than the other important objective, which is to achieve uniformity in the philosophy and structure of fishery management. Each commission has made progress in certain of its objectives, but the general consensus of opinion is that progress has been slow in overcoming the very difficult social-political problems that originally led to the formation of these compacts 12/. A mechanism for better exchange of information between interstate commissions might be useful. The Pacific Marine Fisheries Commission has underway a review of the organization and accomplishments of the three marine fisheries commissions, which may lead to better co-ordination.

The marine fishery commissions have been dominated by commercial fishing interests, although all three give some attention to the problems of the sport fisheries. Growing recreational uses of United States coastal waters are coming into conflict with commercial fishing operations. Public actions to curtail commercial fisheries in inshore waters often invoke conservation as their objective, ignoring the fact that the scientific problem is to determine how great a catch the resource can sustain, not who should take the fish. How the catch should be distributed among those who wish to take it is purely a social-political matter, which has not yet been solved in an objective manner in the United States. It is generally agreed that economic values much enter into such decisions, and the economic values of sport fisheries have been discussed for years by the marine fishery commissions and other bodies. It is fair to state that no acceptable method of deriving comparable economic evaluations of commercial and sport fisheries has yet been developed. Successful management of fishery resources in the United States may well depend upon a solution to this problem.

12/ McHugh, J.L. 1963. Stocktaking for the new regime. Atlantic States Marine Fisheries Commission, 21st Annual Report, pp. 62-65.

2.2 Non-governmental. Fishery research and teaching appear in the curricula of a number of universities and colleges in the United States. The largest program of this kind is in the University of Washington at Seattle, which supports a College of Fisheries, headed by a Dean, with broad programs of instruction in biology and food science. The Institute of Fisheries Research of the College carries out major programs of research, supported primarily by the Federal Government and the State of Washington, and to some extent by the commercial fishing industry. Special research and teaching programs can be arranged by the College to emphasize economic, legal, engineering, or other aspects of fishery problems, by special arrangement with members of other faculties in the University. An example is a recently-completed study of the effects and feasibility of limiting entry of units of gear into the salmon industry 13/. Many other coastal and inland universities and colleges offer training in fishery science, ranging from entire curricula leading to a degree in fisheries to only a single course. A recent survey by the Sport Fishing Institute 14/ identified 106 institutions of higher learning in North America which offer courses in fishery biology or ichthyology.

The fishing industry in the United States supports research indirectly in a number of ways, by providing information on catch and fishing effort, by co-operating in making scientific observations, or by making space available for scientists and technicians aboard fishing vessels or at landing points and processing plants. Some segments of industry support research directly. For example, the Alaska salmon industry was instrumental in establishing the Fisheries Research Institute at the University of Washington and has contributed funds in support of the Institute since its inception. Certain segments of the fishing industry in California have provided funds for research by a voluntary tonnage tax on landings of certain species. In Maine, the Sardine Packers Association has provided research funds by a voluntary tax per case of sardines packed. The Oyster Institute of North America has contributed funds to support fishery research occasionally. There may be other examples, but generally the commercial fishing industry of the United States has not given major financial support to research related to fishery management.

The sport fishing industry also supports fishery research in various ways. For example, The Sport Fishing Institute has awarded 144 graduate research grants or fellowships in fishery biology at 44 colleges and universities for a total amount of more than $206,000.

3. Consultative Machinery

3.1 Within government. The three interstate fisheries commissions, which include in their membership all maritime States except two, have been described already. The only non-member State which fronts on the sea is the newest State, Hawaii. Two inland States also are members: Idaho in the Pacific Marine Fisheries Commission, and Pennsylvania in the Atlantic States Marine Fisheries Commission. Thus, 24 of the 50 States belong to organizations dedicated to co-ordinated research and management of the marine fishery resources in which the Federal Government plays an active part or participates in a consultative capacity 15/.

13/ Royce, W.F. et al, 1963. Salmon gear limitation in northern Washington waters. Univ. of Washington Pubs. in Fisheries, New Series, Vol. 2, No. 1, pp. 1 - 123.

14/ SFI Bulletin No. 159, February 1965, p. 7. See also Appendix X.

15/ Florida belongs to the Atlantic and the Gulf States Marine Fisheries Commissions.

The eight States bordering on the Great Lakes (of which New York and Pennsylvania also belong to ASMFC) co-operate closely with the Federal Government as members or advisors on the United States Section of the international Great Lakes Fishery Commission. In addition to its primary interest, which concerns control of the parasitic sea lamprey, this Commission is developing research plans for each of the five lakes.

The Ohio River Valley Water Sanitation Commission and the Upper Mississippi River Conservation Commission include 12 States in their membership, several of which are members of the Interstate Fishery Commissions or the GLFC. These two interstate river basin commissions also co-ordinate their activities with the Fish and Wildlife Service.

The remaining 15 inland States are not directly associated with the Federal Government in compacts designed to co-ordinate research and management of commercial fisheries. None of these States, however, has an important commercial fishery. Their total landed value in 1962 was less than $2 million, less than 1 percent of the total landed value of all domestic commercial fisheries in that year. If the States in which TVA is located also are excluded, the total annual value of commercial fish landings in the remainder is less than a million dollars. Many of these States have important sport fisheries, as do many States belonging to the marine fisheries compacts or the international Great Lakes Fishery Commission. The inland States in general have oriented their fishery research and other activities towards the sport fisheries. This is only natural, since funds to support fish and game divisions come largely from fishing and hunting fees or from Federal aid programs such as the Dingell-Johnson Act. Research proposed by the States for support under this program is subject to Federal review and approval. This is administered by the Bureau of Sport Fisheries and Wildlife, providing an effective measure of co-ordination.

The Federal Government and the States also co-operate in a variety of other ways in the management of fishery research programs. Under territorial status these activities were handled by the Federal Government, and as the new States of Alaska and Hawaii established their Department of Fish and Game and Division of Fish and Game respectively, the U.S. Fish and Wildlife Service has co-operated by continuing to provide necessary research and services. Strong Federal-State teamwork should persist as these new States continue to strengthen their programs, and the Federal Government alters its activities to provide supporting functions. Alaska also joins with the Pacific North-west States in advising the U.S. Section of the International North Pacific Fisheries Commission. The Great Lakes States, and many of the maritime States, provide advisory services to the U.S. Sections of the various international fishery commissions where their individual interests are concerned.

Most of the 50 States consult formally or informally with each other on problems of common concern. These arrangements may be relatively permanent, with objectives shaped to meet the particular problems with which they were established to deal. This might be co-ordinated planning on a very broad scale, of the kind which characterizes special River Basin studies, such as the Interstate Commission on the Delaware River Basin, the Ohio River Valley Water Sanitation Commission (ORSANCO), or the Upper Mississippi River Conservation Commission. It might have much more restricted objectives, such as the Potomac River Commission 16/, which is concerned primarily with oystering problems of mutual concern to the States of Maryland and Virginia in certain contiguous waters. It might be a purely informal *ad hoc* body, with no statutory authority, formed to develop plans which are placed in effect by legislative or administrative action when called to the attention of the appropriate authority. Or it might be a conference called by the Governor of a State, such as the 1961 and 1963

16/ Public Law 87-783, 87th Congress, House Joint Resolution 659, October 10, 1962. 76 Stat. 797.

Governors' Conferences on Pacific salmon 17/. The Federal Government plays various roles in the work of such groups, from formal arrangements whereby a full-time executive secretary is provided, as is done by the Bureau of Sport Fisheries and Wildlife for the Upper Mississippi River Conservation Commission, or where a Federal Government representative sits as a commissioner, as does a scientist-administrator of the Bureau of Sport Fisheries and Wildlife on ORSANCO.

Although the U.S. Fish and Wildlife Service of the Department of the Interior is the Federal agency with primary responsibility for fishery research, several other Federal Departments and agencies have an interest in these matters. The Federal Water Pollution Control Administration, recently transferred to the Department of the Interior from the Department of Health, Education, and Welfare, plans at least two research centers, one on the Atlantic coast and one on the Great Lakes, which will study the effects of pollution upon aquatic life. The Public Health Service of the Department of Health, Education and Welfare has very broad responsibilities which conconcern transmission of disease, toxins, or other harmful elements from shellfish and other fishery products to humans. The authority of the Public Health Service is very broad, and the Department has chosen to interpret its mission as including research on the effects of these factors upon the aquatic organisms themselves. Thus, the PHS conducts research upon the effects of pesticides and other pollutants upon growth, survival, and other characteristics of marine and freshwater life, just as do the two Bureaux of the Fish and Wildlife Service. The Food and Drug Administration (FDA) of HEW also has an interest in the quality of fishery products as human food and in the effects of pollutants and toxins on the living resources themselves. Other Federal agencies with important interests in fishery research are the Atomic Energy Commission (AEC), in matters relating to the effects of radioactivity and radioactive wastes upon aquatic resources; the Corps of Engineers of the U.S. Army, in relation to the effects of dams and other engineering structures on fisheries; and the Department of State, in relation to international fishery problems. Their support may be in the form of contracts with the Department of the Interior for support of laboratories, such as the AEC support of the Radiobiological Research Laboratory of the Bureau of Commercial Fisheries at Beaufort, N.C., or Corps of Engineers support of the BCF Fish Passage Field Laboratory at Bonneville, Washington. The State Department maintains a staff of fishery experts in the Office of the Under Secretary of State, supports the staffs of international fishery commissions, and organizes and supports various international fishery conferences.

3.2 Between government and non-governmental institutions. The quality of consultative machinery at this level varies greatly, depending upon local circumstances. Many examples of Federal relationships with universities and private institutions have been given already. In some cases this collaboration includes financial support, such as the current Federal Government support of research (and incidentally graduate instruction) in the Institute of Fisheries at the University of Washington, the Institute of Marine Resources of the University of California, and the Division of Fisheries of the Institute of Marine Science of the University of Miami. The Bureau of Commercial Fisheries supports graduate students in a variety of disciplines at selected American universities (Table 7). The Bureau of Sport Fisheries and Wildlife supports co-operative fishery units 18/at 13 universities (Table 8). University professors are retained as consultants to advise on award of fellowships, planning and conduct of research, and other matters relating to fishery research.

Similar relationships exist between State and private agencies and institutions. In some States, such as Virginia, Maryland, and North Carolina, the State fishery research program is carried out by colleges or universities or in institutions closely associated with universities. In Virginia, State-supported fishery research and

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17/ First Governor's Conference on Pacific Salmon, Juneau, Alaska, Feb. 1961.
Second Governor's Conference on Pacific Salmon, Seattle, Washington, Jan. 1963.

18/ King, Willis. 1962. The Cooperative Fishery Units. Prepared for the meeting of the Southern Division, American Fisheries Society, Charleston, South Carolina. October 15-17, 1962.

TABLE 7. BUREAU OF COMMERCIAL FISHERIES GRADUATE EDUCATIONAL GRANTS IN AQUATIC SCIENCES

No.	University	1961-62 No. of Grants	1961-62 No. of Stud.	1962-63 No. of Grants	1962-63 No. of Stud.	1963-64 No. of Grants	1963-64 No. of Stud.	1964-65 No. of Grants	1964-65 No. of Stud.	Total No. of Grants	Total No. Indivd. Students
1	California, Berkeley	-	-	-	-	-	-	1	1	1	1
2	California, Scripps	-	-	2	2	2	4	2	4	6	6
3	Columbia, Lamont Geol.Obs	-	-	-	-	-	-	1	1	1	1
4	Cornell	-	-	-	-	-	-	1	1	1	1
5	Duke	-	-	1	1	1	3	1	3	3	5
6	Florida State	-	-	-	-	1	1	-	1	1	2
7	Hawaii	-	-	1	1	1	2	1	2	3	3
8	Iowa State	-	-	-	-	1	1	1	2	2	2
9	Johns Hopkins	-	-	1	1	1	2	1	2	3	3
10	MIT	-	-	1	1	-	1	2	2	3	2
11	Massachusetts	-	-	-	-	1	1	-	1	1	1
12	Miami	1	1	2	2	3	4	2	4	8	6
13	Michigan	-	-	1	1	1	2	2	3	4	4
14	Michigan State	-	-	-	-	1	1	-	1	1	1
15	New York	-	-	-	-	1	1	-	1	1	1
16	North Carolina State	-	-	-	-	1	1	-	1	1	1
17	North Dakota	-	-	-	-	-	-	1	1	1	1
18	Oregon State	-	-	2	2	2	4	2	4	6	6
19	Rhode Island	-	-	1	1	1	2	1	2	3	4
20	Rutgers	-	-	-	-	1	1	-	1	1	1
21	Texas A and M	-	-	1	1	-	1	-	1	1	1
22	Texas	-	-	-	-	1	1	-	1	1	1
23	Virginia	-	-	-	-	-	-	1	1	1	1
24	Washington	-	-	3	3	2	6	3	6	8	12
25	Wisconsin	-	-	-	-	-	-	1	1	1	1
26	Yale	-	-	1	1	-	1	-	-	1	1
	Totals	1	1	17	17	22	40	24	48	64	69

TABLE 8

BUREAU OF SPORT FISHERIES AND WILDLIFE
DIVISION OF FISHERY MANAGEMENT SERVICES

CO-OPERATIVE FISHERY UNIT LEADERS AND ASSISTANT LEADERS AS OF SEPTEMBER 16, 1964

(Dates of establishment in parentheses)

Region 1	Montana State College, Bozeman, Montana (1964) Leader - Dr. Richard Graham Assistant - Dr. William R. Gould, Jr.
	University of Idaho, Moscow, Idaho (1964) Leader - Dr. Donald Chapman Assistant - Robert N. Thompson
Region 2	Utah State University, Logan, Utah (1962) Leader - Dr. Donald R. Franklin Assistant -
	Colorado State University, Fort Collins, Colorado (1963) Leader - Dr. Robert Vincent Assistant - Dr. George Post
	University of Arizona, Tucson, Arizona (1965) Leader - Dr. William McConnell Assistant -
Region 3	University of Missouri, Columbia, Missouri (1963) Leader - Dr. Richard Anderson Assistant - David Foster
Region 4	Louisiana State University, Baton Rouge, Louisiana (1963) Leader - Dr. Renford O. Smitherman Assistant - William Herke
	University of Georgia, Athens, Georgia (1963) Leader - Dr. Roger Barnhart Assistant - Melvin R. Huish
	North Carolina State College, Raleigh, North Carolina (1963) Leader - Dr. F. Eugene Hester Assistant -
Region 5	University of Maine, Orono, Maine (1963) Leader - Dr. Richard Hatch Assistant - Dr. Paul A. Haefner, Jr.
	University of Massachusetts, Amherst, Massachusetts (1964) Leader - Dr. James McCann Assistant - Dr. Roger J. Reed
	Cornell University, Ithaca, New York (1964) Leader - Dr. Alfred W. Eipper Assistant - Dr. Henry Regier

Pennsylvania State University, University Park, Pennsylvania (1964)
Leader - Dr. Robert L. Butler
Assistant - Anthony Bodola

Public Law 86-686
86th Congress, S. 1781
September 2, 1960

AN ACT — 74 Stat. 733.

To facilitate co-operation between the Federal Government, colleges and universities, the States, and private organizations for co-operative unit programs of research and education relating to fish and wildlife, and for other purposes.

Fish and Wildlife. Co-operative unit programs.

Be it enacted by the Senate and House of Representatives of the United States of America in Congress assembled, That, for the purpose of developing adequate, co-ordinated, co-operative research and training programs for fish and wildlife resources, the Secretary of the Interior is authorized to continue to enter into co-operative agreements with colleges and universities, with game and fish departments of the several States, and with nonprofit organizations relating to co-operative research units: Provided, That Federal participation in the conduct of such co-operative unit programs shall be limited to the assignment of Department of the Interior technical personnel by the Secretary to serve at the respective units, to supply for the use of the particular units' operations such equipment as may be available to the Secretary for such purposes, and the payment of incidental expenses of Federal personnel and employees of co-operating agencies assigned to the units.

Appropriation

Sec. 2. There is authorized to be appropriated such sums as may be necessary to carry out the purposes of this Act.

APPROVED September 2, 1960.

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graduate teaching are done in the same institution by the same staff, to the benefit of both activities. In other States the universities and State fishery agencies are in competition with each other for State and Federal research funds, often to the detriment of both. There is no standard pattern, although to some extent the interstate fishery commissions provide a machinery for consultation between Federal, State, university, and privately supported fishery research.

3.3 Between government, industry, and other segments of the community. The two Bureaux of the Fish and Wildlife Service maintain various formal and informal relationships with industry and other public groups. The American Fisheries Advisory Committee (AFAC) meets twice a year with the Assistant Secretary for Fisheries and Wildlife and the Director and staff of Bureau of Commercial Fisheries to review plans and programs and recommend problems which require attention. The Bureau maintains contacts with a variety of national and local trade organizations, fish processors, and fishermen's unions, such as the National Fisheries Institute, Shrimp Association of the Americas, National Fish Meal and Oil Association, National Canners Association, Oyster Institute of North America, and Association of Pacific Fisheries, to name only a few. A complete listing of such organizations and associations is published annually by the National Wildlife Federation 19/.

19/ Conservation Directory, 1964-65. A Listing of Organizations, Agencies, and Officials Concerned with Natural Resource Use and Management. National Wildlife Federation, 1412 16th Street, N.W., Washington, D.C., iv + 106 pp., 1964.

The Bureau of Sport Fisheries and Wildlife has similar associations with commercial and public groups. Relationships are particulary close with the American Association of Fishing Tackle Manufacturers; the Trout Growers of America, an association of commercial trout producers; and the Sport Fishing Institute, an organization sponsored principally by manufacturers of fishing tackle. The Sport Fishing Institute has been effective in the fight for enlightened fishery management, appointment of professional fishery experts rather than political appointees to leading Federal and State positions, and improved qualification standards and salaries for fishery scientists.

The Bureau of Sport Fisheries and Wildlife also works closely with many private conservation agencies of national or local interest. The Izaac Walton League, the National Wildlife Federation, and Resources for the Future are but three examples of import national bodies interested in fishery research 20/. Most States have several national bodies. Some are banded together with centralized organizations with permanent Secretariats, like the Sportsmen's Clubs of Texas, the Michigan United Conservation Clubs, and other such affiliates of the National Wildlife Federation. Some States have recognized the importance of their sport fishing resources by establishing permanent offices supported, at least in part, by State funds. Such an organization is the Virginia Salt Water Sport Fishing Association, which generates publicity, sponsors fishing tournaments, and establishes liaison with public and private agencies and associations having similar interests. Both Bureaux of the Fish and Wildlife Service, the U.S. Public Health Service, and other Federal agencies, the interstate fishery and river basin commissions, and interested elements of State Governments, all maintain contact and assist in the work of these private and semi-official State groups.

4. Formulation of Research Objectives

National objectives of research on commercial and sport fishery problems are supported by the Fish and Wildlife Act of 1956 (Appendix II) and a variety of other statutory authorities, some general, some specific. Recently, both Bureaux of the Fish and Wildlife Service have reviewed their statutory authorities and responsibilities and have developed long-range programs of research, development, and services. "Operation Trident", the program of the Bureau of Commercial Fisheries 21/, is an approved document, backed up by more detailed programs published by the Regional and Area Offices of the Bureau 22/. These programs were reviewed by, and discussed extensively with, industry members and State officials before publication. The long-range program of the Bureau of Sport Fisheries and Wildlife has not yet been approved for publication. Recently, a new system of program planning and budgeting (PPBS) has been adopted by the Federal Government, which attempts to express the output of all Federal activities in economic terms and weighs the value of alternative uses of the resources available. It is too early to judge the applicability of this system to fishery research.

The interstate fishery commissions, especially the Atlantic States Marine Fisheries Commission and the Gulf States Marine Fisheries Commission, often establish Federal research objectives by resolutions requesting the Federal Government to undertake certain research projects. The recent ten-year study of shad on the Atlantic coast came about through such a resolution of ASMFC, and it was later requested by the Commission and agreed by the Government, that the funds be diverted to research on the blue crab resource as the shad program terminated. Many other organizations, representing groups of commercial or sport fishermen, make similar recommendations from time to time. Such requests are given serious consideration when program objectives are reviewed.

20/ Conservation Directory, 1964-65. A listing of Organizations, Agencies, and Officials Concerned with Natural Resource Use and Management. National Wildlife Federation, 1412 16th Street, N.W., Washington, D.C., ix + 106 pp., 1964.

21/ Operation Trident. U.S. Dept. of the Interior, Bureau of Commercial Fisheries, Circular 142. Washington, D.C., April 962, 132. pp.

22/ Circulars 147, 164, 171 and 181 of the Bureau of Commercial Fisheries.

Fishery research objectives of the Federal Government often are established by direct or indirect action of the Congress. One such route is by a bill or resolution introduced in one of the Houses of Congress. Such a bill, if enacted into law, expresses the desire of the Congress and the Executive that a particular research objective be adopted. Funds to do the work must be provided through the normal appropriation process. A more direct method is by addition of funds to the Federal budget as it passes through the Congress. This usually is done in the Senate, often at the request of commercial or sport fishing interests.

5. Governmental Planning of Research

5.1 Nomination of projects. Several methods by which research projects or programs can be established have been outlined in the previous section. Federal plans, which originate as recommendations of public or private groups, or in the Congress, usually call for short-range projects aimed at solving immediate problems. Plans for long-range basic studies often originate at the working level, frequently on the recommendation of individual scientists. Such plans are difficult to translate into action unless they also receive strong public support, and this support seldom is forthcoming for basic research. For years fishery research in the United States has suffered from a lack of the public support necessary to provide proper balance between short-term and long-term objectives.

In the past five years this inbalance has been overcome to a considerable degree by the activities of the Committee on Oceanography of the National Academy of Sciences and the National Research Council (NASCO). Over a period of several years this Committee (Table 9) reviewed the status of oceanographic knowledge in the United States and the future needs of the nation in oceanographic research and produced a detailed 10-year program 23/. Not content to consider its work done when it had completed its report and recommended Federal support of the proposed program, NASCO turned its attention to the next step. Working closely with the appropriate Federal Departments, specialized agencies, and the Congress, the Committee succeeded in gaining Federal support of its recommendations. The Interagency Committee on Oceanography (ICO) was established to co-ordinate the many oceanographic research activities of the Federal Government (Tables 6 and 10). As a result, the budget of the Fish and Wildlife Service for marine fishery research has approximately tripled in the last five years, and the importance of basic research for promoting conservation of fishery resources now receives more equitable attention. NASCO plans to give continued attention to the progress of its program in the Federal Government, for primary attention has been given to construction of adequate research facilities in the form of new laboratories and ships. Although this construction program is well advanced, it has not yet reached completion. Meanwhile, other demands on Federal funds threaten to halt parallel development of research programs and are making it difficult to utilize the new facilities fully. A study of the economic advantages to be gained from oceanographic research has been completed recently 24/.

The importance of fishery research in the U.S. National Oceanographic Program is indicated by the fact that the present chairman of NASCO, Dr. Milner B. Schaefer, is a fishery scientist.

5.2 Development of research plans. In the Fish and Wildlife Service the exact nature of research programs is determined by Laboratory Directors and their scientific staffs. Each laboratory has a mission, established in general terms by the Central

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23/ Oceanography 1960 to 1970. A report of the Committee on Oceanography, National Academy of Sciences - National Research Council. 12 Chapters published separately, 1959-1962.

24/ Economic benefits from oceanographic research. National Academy of Sciences - National Research Council, Pub. No. 1228, 1964, 50 pp.

TABLE 9

NATIONAL ACADEMY OF SCIENCES COMMITTEE ON OCEANOGRAPHY

Membership List, June 1966

Dr. Karl Banse
Department of Oceanography
University of Washington
Seattle, Washington

Dr. Wayne V. Burt
Department of Oceanography
Oregon State University
Corvallis, Oregon

Dr. Paul M. Fye
Woods Hole Oceanographic
Institution
Woods Hole, Massachusetts

Dr. John Knauss
University of Rhode Island
Narragansett Marine Laboratory
Kingston, Rhode Island

Mr. Sumner Pike
Lubec, Maine

Dr. Donald W. Pritchard
Chesapeake Bay Institute
Johns Hopkins University
Baltimore, Maryland

Dr. Roger R. Revelle
Center for Populations Studies
Harvard School of Public Health
9 Bow Street
Cambridge, Massachusetts

Dr. Milner B. Schaefer
Institute of Marine Resources
Scripps Institution of
Oceanography
La Jolla, California

Dr. Athelstan S. Spilhaus
Institute of Technology
University of Minnesota
Minneapolis, Minnesota

Prof. Henry Stommel
Massachusetts Institute
of Technology
Room 54-1416
Cambridge, Massachusetts

Dr. George P. Woollard
Hawaii Institute of Geophysics
University of Hawaii
Honolulu, Hawaii

Office in Washington. The scope of each laboratory program is determined by limitations imposed by available funds and facilities, the research capabilities of the staff, and the capacities of non-Bureau organizations which might perform some of the research by contract. When programs are formulated in the laboratory they are endorsed by Regional Directors as to fiscal soundness and relation to other Bureau and non-Bureau fishery activities in the Region. Approval by the Bureau Director is contingent upon advice from his staff as to their scientific merit and their consonance with Bureau policies, objectives, and capa ilities. Long-range planning at Bureau, Regional, and Laboratory levels is an integral part of this process. These procedures preserve to a considerable extent the freedom of the Federal fishery research agencies to remain objective in planning their research programs. This happy situation has been reinforced since 1956 by the appointment of competent and experienced professionals as Directors of Bureaux of the Fish and Wildlife Service. The extent to which the Bureau Directors can maintain objectivity in their research planning, of course, depends upon their ability to adjust to the direct and indirect pressures which are constantly in play through the Executive Branch, the Congress, and various State and public agencies and groups.

In the States the same general procedures prevail. There may be considerable deviation from objectivity, depending upon local circumstances. In many States the State legislature has the power to direct the nature and course of research, either through the appropriation process or through direct legislation. It is not unusual for legislatures to set up special groups or commissions to deal with particular fishery problems or to review the research program in general. Often, the research arm of State fishery agencies is under political rather than professional supervision. These need not be handicaps, but under certain circumstances such dominance can and does create shifting policy and deterioration of fishery research and management.

Development of fishery research ideas and plans, at the Federal and State level, is stimulated through a variety of channels of communication with the commercial fishing industry, sport fishermen, and the scientific community. These interacting mechanisms are numerous and varied, some formal and permanent, other completely informal and ad hoc. The formal arrangements are described elsewhere in this document. Examples of informal arrangements are the annual Eastern Pacific Oceanic Conference (EPOC) and the Pacific Tuna Conference on the west coast of North America. More formal, but of a similar nature, is the annual conference sponsored by the California Co-operative Oceanic Fisheries Investigations (CalCOFI). The EPOC Conference brings together fishery scientists, oceanographers, and meteorologists engaged in studies of air-sea interactions, oceanographic conditions and processes, and the ocean as an environment of fishing resources. Attendance includes scientists and administrators from Federal, State, university, and private institutions in the United States, including Alaska and Hawaii, Canada and Latin America. A few representatives of the fishing industry also attend. The Pacific Tuna Conference includes Federal, State, and academic scientists working on Pacific tunas. The annual CalCOFI Conference brings together marine scientists studying the fishery resources of the California Current, but scientists from Europe, Japan, and elsewhere sometimes attend on invitation. Many other conferences of scientists, administrators, and political and industry representatives are necessary to co-ordinate planning of fishery research in the United States.

Probably nowhere else in the world is there such a division of responsibility for fishery research and related scientific investigations among a variety of Federal, State, and other organizations as there is in the United States. This is confusing not only to elements in the United States such as the Bureau of the Budget in the Executive Branch, and the Congress, but also to foreign observers. In some ways, it is surprising that this division of responsibility works as well as it does. Indeed, it has certain advantages, not the least of which is the freedom it provides for some elements of the research structure to avoid hasty judgments in planning research and solving fishery problems, and to pursue long-range basic studies. On the other hand, the amount of effort necessary to accomplish mutual understanding and co-operation is

TABLE 10

INTERAGENCY COMMITTEE ON OCEANOGRAPHY

Membership List, June 1966

DEPARTMENT OF DEFENSE

Member:	Hon. Robert W. Morse, Chairman Assistant Secretary of the Navy for Research and Development
Assistant:	Capt. J. Edward Snyder, Jr., USN Executive Assistant to the Chairman
Alternate:	RADM Odale D. Waters, Jr. Oceanographer of the Navy U.S. Naval Oceanographic Office

ATOMIC ENERGY COMMISSION

Member:	Dr. John N. Wolfe, Chief Environmental Sciences Branch Division of Biology and Medicine

DEPARTMENT OF COMMERCE

Member:	VADM H. Arnold Karo Deputy Administrator Environmental Science Services Administration

DEPARTMENT OF HEALTH, EDUCATION AND WELFARE

Member:	Mr. Harry G. Hanson Associate Chief for Environmental Health Public Health Service

DEPARTMENT OF THE INTERIOR

Member:	Mr. Donald L. McKernan, Director Bureau of Commercial Fisheries
Alternate:	Dr. J L. McHugh Assistant Director for Biological Research Bureau of Commercial Fisheries

NATIONAL SCIENCE FOUNDATION

Member:	Dr. Harve J. Carlson Assistant Director for Biological and Medical Sciences
Alternate:	Dr. William E. Benson, Head Earth Sciences Section

SMITHSONIAN INSTITUTION

Member:	Dr. I. E. Wallen Assistant Director for Oceanography Museum of Natural History

DEPARTMENT OF STATE

Member:	Mr. Herman Pollack Acting Director International Scientific and Technological Affairs
Alternate:	Mr. William H. Littlewood Science Officer International Scientific and Technological Affairs

DEPARTMENT OF THE TREASURY

Member:	RADM F. V. Helmer, Chief Office of Operations U.S. Coast Guard Headquarters

enormous. It tends to drain off the energies of many of the most competent professionals from direct participation in research planning. It may lead also to compromise solutions not conducive to scientific creativity.

The Bureau of Commercial Fisheries has adopted a detailed system of program planning and control which is described fully in Bureau Administrative Order No. 77. This is now being superseded by the new Program Planning and Budgeting System (PPBS) referred to previously.

In the individual States, program planning procedures vary widely. Characteristically, however, general procedures are much less formal than in the Federal Government. Co-ordination of planning is achieved through the interstate fishery or river basin commissions for member States, or in small permanent or ad hoc commissions or committees.

5.3 Source and allocation of funds. Most Federal funds for fishery research are provided by direct appropriation, principally in the budgets of the Department of the Interior, but also in the Department of State. The Bureau of Commercial Fisheries currently spends about $18 million a year and the Bureau of Sport Fisheries and Wildlife nearly $3 million a year on fishery research. The Corps of Engineers of the United States Army, the Atomic Energy Commission, and some other government agencies, provide funds for certain specialized studies, usually by contract with the Department of the Interior, the individual States, or university and private laboratories.

In 1954 the President approved an Act, commonly called the Saltonstall-Kennedy Act [25], which provided that an amount equal to 30 percent of the gross receipts from import duties on fishery products be transferred each year to the Secretary of the Interior to promote the free flow of domestically produced fishery products in commerce. This produces an annual fund of about $5 million, a substantial part of which supports commercial fishery research. Originally these funds were considered to be available for short-term studies of immediate application to problems of the fishing industry. It was generally believed also that most of these funds would be used to support research under contract with the individual States. From time to time, however, the Bureau was directed by the Executive Branch or by the Congress to use the monies in support of its own program. Consequently, only a small part of these funds is used by the States.

In 1963 the Congress passed a bill which would appropriate annually $5 million to support commercial fishery research and development in the States. The Act (Public Law 88-309) provides that these funds will be allotted on a matching basis to the States according to a formula which takes into account the value of their individual landings.

The Dingell-Johnson Act, approved in 1950, provides that a portion of the funds collected through Federal excise taxes on fishing tackle be transferred to the Secretary of the Interior to assist the States to restore their sport fish populations. The funds so derived are allotted as grants to the States, on a matching basis, according to a formula based on relative land area and numbers of paid fishing licence holders. A considerable portion of these funds is spent on sport fish research.

State-supported fishery research is financed in a variety of ways. Sources of Federal funds have been described above. Some States derive almost all their fishery research funds by direct appropriation, others from special funds created by fishing licence fees or other special levies.

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[25] Saltonstall-Kennedy Act, as amended. (An excerpt from Title 15 of the United States Code.) U.S. Dept. of the Interior, Bureau of Commercial Fisheries, Fishery Leaflet No. 556, Sept. 1963, 2 pp.

5.4. Staffing. Classification and salary scales of fishery research biologists in the Federal Government are given in Table II. Laboratory Directors are GS-14 or GS-15 in grade, and Program Chiefs GS-12,-13,or-14. Biologists with a bachelor's degree usually are recruited at the GS-7 level, master's at GS-9, and newly-awarded doctorates at GS-11 or GS-12. Scientists with special qualifications or outstanding achievements may be advanced to grades higher than GS-15 or to positions outside the Civil Service Classification Act under Public Law 80-313, with salaries as high as $24,500. Promotion to these "super grades" may be effected entirely on the basis of scientific achievement, and the holder of such a grade does not need to assume onerous administrative duties in order to qualify. These progressive policies have brought a considerable revision of the distribution of grades and salaries for Federal fishery scientists in the past decade. However, the average grade of fishery scientists in the Federal Government still is below the averate grade for most other scientists in the Federal Service. The Fish and Wildlife Service therefore is not fully competitive with other Federal agencies for the services of scientists.

With few exceptions, the States are at a disadvantage vis a vis the Federal Government in salary scales for scientists. In many States this has affected the quality of research staffs and programs. The representative State salary schedules in Table 12 clearly demonstrate the discrepancy between Federal and State salaries, and the wide variation among the States. Yet State agencies like the Virginia Institute for Marine Research (VIMS) by reason of their association with leading academic institutions and considerate administrative autonomy, have been able almost to keep pace with the Federal Government in salary scales for scientists. Salaries of scientists at VIMS are as follows: Director $14,000; Senior Scientist $10,032 - $12,528; Marine Scientist C $8,400 - 10,512, B $7,032 - $8,784, A $5,880 - $7,344. In Virginia, this gives the marine fishery research agency a distinct advantage over the freshwater agency in recruiting scientists.

It is Federal Government policy to give preference to scientists holding the doctorate degree in senior scientific administrative positions. Most laboratory directors and many program chiefs have Ph.D.'s. About one in seven scientists in the Bureau of Commercial Fisheries holds the doctorate.

Training of fishery scientists is receiving increasing attention, especially in the Federal Government. The Bureau of Commercial Fisheries supports about 40 graduate students per year at various universities throughout the United States. The Bureau of Sport Fisheries and Wildlife supports a smaller number of graduate students in fisheries. Both Bureaux have authority to establish co-operative fishery units at universities and the Bureau of Sport Fisheries and Wildlife has already established several such units. Several research laboratories of the Bureau of Commercial Fisheries are located on the campuses of universities or collaborate closely with universities. Senior staff members of these laboratories usually hold faculty rank at these institutions of higher learning. The Bureaux also are able to offer training programs of various kinds to their own staff members, paying tuition fees and other expenses, and retaining employees on full pay for periods as long as one year to continue their education.

5.5 Time tables. The Federal fishery research program is based on long-range planning and a detailed program planning and control system. The system in effect in the Bureau of Commercial Fisheries has been mentioned already. Research programs and projects may have short-term or long-term objectives, but whenever possible these are subdivided into phases with clear-cut termination points. Even a continuing activity like collection of statistics on landings has an annual goal, which is marked by publication of a detailed annual summary 26/.

26/ Power, E.A. and C.H. Lyles, 1964. Fishery Statistics of the United States 1962. U.S. Dept. of the Interior, Bureau of Commercial Fisheries, Statistical Digest 56:466 pp.

TABLE 11

SCHEDULE OF ANNUAL FEDERAL GOVERNMENT PROFESSIONAL SALARY RATES BY GRADE EFFECTIVE OCTOBER 10, 1965

GRADE	RATES WITHIN GRADE AND WAITING PERIOD FOR NEXT STEP INCREASE									
	52 Weeks			104 Weeks			156 Weeks			
	1	2	3	4	5	6	7	8	9	10
5	5,181	5,352	5,523	5,694	5,865	6,036	6,207	6,378	6,549	6,720
7	6,269	6,476	6,683	6,890	7,097	7,304	7,511	7,718	7,925	8,132
9	7,479	7,733	7,987	8,241	8,495	8,749	9,003	9,257	9,511	9,765
11	8,961	9,267	9,573	9,879	10,185	10,491	10,797	11,103	11,409	11,715
12	10,619	10,987	11,355	11,723	12,091	12,459	12,827	13,195	13,563	13,931
13	12,510	12,945	13,380	13,815	14,250	14,685	15,120	15,555	15,990	16,425
14	14,680	15,188	15,696	16,204	16,712	17,220	17,728	18,236	18,744	19,252
15	17,055	17,645	18,235	18,825	19,415	20,005	20,595	21,185	21,775	22,365
16	19,619	20,297	20,975	21,653	22,331	23,009	23,687	24,365	25,043	
17	22,217	22,994	23,771	24,548	25,325					
18	25,382									

TABLE 12

SALARY SCALES OF FISHERY SCIENTISTS IN SELECTED STATES IN 1963 27/

	Fishery Chief	Senior Biologist	Junior Biologist
Michigan	12,340 - 15,534	5,742 - 7,224	5,804 - 6,013
California	11,520 - 13,992	8,604 -10,440	5,556 - 6,744
Maine	12,500	5,954 - 7,228	5,148 - 6,240
New York	9,980 - 11,960	7,350 - 8,895	5,910 - 7.205
Montana	10,272	7,380 - 8,532	5,328 - 6,288
Washington	8,964 - 10,704	6,324 - 7,524	5,544 - 6,600
Florida	8,280 - 10,560	6,000 - 7,560	4,560 - 5,760
Virginia	8,400 - 10.032	5,400 - 8,040	———
Maryland	7,800 - 9,750	6,660 - 8,323	5,040 - 6,302
Oklahoma	6,600 - 8,400	5,160 - 6,360	4,320 - 5.400
Mississippi	7,300	6,000 - 6,300	4,800 - 5,700

27/ Compiled by Sport Fishing Institute

No standard interstate system of program schedules is in effect. Often, fishery research programs in the States are of a short-term nature. The degree of internal control varies widely, from systems comparable to those in effect in the Federal Government to almost complete lack of control. In many States priorities are determined on the basis of urgency and are subject to influence from various sources. State legislatures generally have sweeping powers over research programs, which they can exert by direct legislation or by control of appropriations. Changes in administration often create fundamental changes in policy, and these are just as likely to affect research programs adversely as beneficially. The effects of adverse changes can be corrected only slowly. In States where such upheavals are frequent, the quality of research is poor and it is almost impossible to retain or recruit well-qualified staffs.

The Bureau of Commercial Fisheries also is developing a corps of senior scientists. These are scientific employees of long standing who by reason of unusual scientific competence and achievement have earned the privilege of being freed of administrative duties in order to carry out independent activities of interest to the Bureau and the Government. These leading scientists conduct independent research in their own fields of specialization, publish comprehensive review papers or reference books on broad fields of fishery science, offer consultative services on request from Federal, State or private agencies, or lecture and supervise graduate study at universities. This arrangement has already produced some outstanding scientific contributions 28/.

6. Conduct of Research

In the Bureau of Commercial Fisheries, operations are organized on a staff and line basis. The small administrative staffs of the Divisions of Biological and Industrial Research in Washington, D.C., develop policy guidelines and review programs and budgets, but seldom exert direct line authority over field operations. Administrative control over laboratories and field operations is provided by six regional offices and one area office. Regional staffs are small and do not contain counterparts of the technical division staffs in Washington. Hence, laboratory directors are expected to exercise broad control over planning and conduct of research. When special circumstances warrant, the Washington office may take a direct hand in program matters, but it is general Bureau policy to select competent staffs and to allow these staffs wide latitude in planning and conducting research. For these reasons the Central Office in Washington exercises strong control over the selection of laboratory directors and program chiefs.

Laboratories which conduct major research for international fishery commissions have somewhat less freedom in planning and conducting research. Most of the research program of the Biological Laboratory in Seattle, Washington, is subject to detailed review by the International North Pacific Fisheries Commission and to a considerable degree of control by the U.S. Section of the Commission, which includes industry advisors. The program of the Marine Mammal Research Laboratory in Seattle is controlled largely by the needs of the North Pacific Fur Seal Commission. Similarly, considerable portions of the work of the Biological Laboratories at Ann Arbor, Michigan, and Woods Hole, Massachusetts, are controlled by the special requirements of the Great Lakes Fisheries Commission and the International Commission for Northwest Atlantic Fisheries, respectively.

28/ Loosanoff, Victor L. and Harry C. Davis, 1963. Rearing of bivalve Mollusks. In: Advances in Marine Biology, Vol. 1. Academic Press Ltd., London. England, pp. 1-136.

Galtsoff, Paul S. 1964. The American Oyster. U.S. Dept. of the Interior, Bureau of Commercial Fisheries, Fishery Bulletin Vol. 64, iii + 480 pp.

The smaller fishery research programs of the Bureau of Sport Fisheries and Wildlife receive a greater degree of line supervision from the Washington office. This is the responsibility of the Chief of the Division of Fishery Research.

Generally, of course, Federal fishery research programs must be responsive to the desires and needs of the Congress, the Executive, and commercial or sport fish interests. These controls are executed through policy directives, legislation, advisory committees, and various public groups, as described previously.

Controls exerted over conduct of research in the States vary widely. When programs are financed through Federal grants or contracts, as under the Dingell-Johnson Act or Public Law 88-309, proposals are subject to review by the Department of the Interior, and continuation of a particular piece of research is contingent upon satisfactory performance. Similar controls are exerted by agencies like the Army Corps of Engineers or Atomic Energy Commission over contracts with other Federal or State agencies. Within the individual States conduct of research may be reviewed and influenced by various bodies, depending upon the form of organization. Generally, the principal groups which show an interest at the State level are the Legislature, the Executive Branch of the State Government, commercial and sport fishing interests, industries which may come in conflict with fishery interests, the universities and colleges within the State, and various smaller institutions, firms, counties, towns, or individuals which have direct or indirect interests in the fisheries. These interrelationships and conflicting pressures often become very complex.

7. Application of Results

Because the States control fishery management within territorial waters, the results of much of the biological fishery research done by the Federal Government is not applied by Federal agencies to the solution of fishery problems. The results of such research is made available to the States through the interstate fishery commissions or directly by contact with the research or enforcement agency. Federal scientists give testimony at Legislative or public hearings, or in courts of law, as requested. Findings also are communicated at meetings of scientists, commercial or sport fishermen, service clubs and trade organizations. The press, radio and television, trade and sportsmens' journals, and conservation magazines are valuable media also.

The commercial fishing industry has been slow to adopt the findings of biologists. This is particularly true in the shellfish industry, where a vast accumulation of scientific and technical knowledge is available to solve several major problems if it were only used systematically by shellfish growers and managers. These problems were discussed in detail at Congressional hearings in October 1963 [29]. To remedy this failure to use existing scientific knowledge the Bureau of Commercial Fisheries established the nucleus of a Shellfish Advisory Service in 1963 [30]. In addition to the reluctance of conservative shellfish planters to put scientific recommendations to use, serious obstacles often are created by restrictive State laws, many of which are contrary to free application of scientific findings, but strongly rooted in local traditions. This discouraging situation will not be corrected quickly. Unfortunately, like many social advances, this revolution may not come about until the situation deteriorates so completely that the sources of the institutional barriers virtually disappear.

29/ Molluscan Shellfish. Hearings before the Subcommittee on Fisheries and Wildlife Conservation of the Committee on Merchant Marine and Fisheries, House of Representatives, 88th Congress, 1st Session, Oct. 2-3, 1963. Serial No. 88-13. U.S. Govt. Printing Office, Washington, D.C. V + 229 pp.

30/ Engle, James B. 1963. Shellfish Advisory Service - Co-operation with the industry. Proceedings Gulf and Caribbean Fisheries Institute, 16th Annual Session, Nov. 1963, pp. 79-83

The lack of uniformity and consistency in State laws is well illustrated by a recent compilation prepared by the Great Lakes Fishery Commission [31]. The bewildering array of size limits, mesh sizes, and closed areas summarized in this report is characteristic of almost any region of the United States where two or more States share the fishery resources of adjacent waters.

Direct application of the findings of biologists often is made most effectively in the international commissions. Here, the objectives usually are relatively narrow and clearly defined and legal and social barriers to application of results usually are superseded by the implementing legislation. Even with these simplifications the application of research findings is not easy. Nevertheless, State Governments and fishery interests could well learn some lessons from the work of the international fishery commissions, imperfect though they are.

8. Reporting and Publications

Publication of the results of fishery research in the United States is not well co-ordinated. The official scientific journals of the Fish and Wildlife Service are the Fishery Bulletin, Fishery Industrial Research, Special Scientific Reports - Fisheries, and Research Reports. Although these journals have not been designated officially as belonging to one Bureau or the other, the first three have come to be recognized as journals of the Bureau of Commercial Fisheries, and the fourth as the fishery research journal of the Bureau of Sport Fisheries and Wildlife. The Fish and Wildlife Service also publishes three series at irregular intervals: Circulars, Conservation Notes, and Fishery Leaflets. Other publications of the Bureaus are listed in Table 13.

Several States publish journals or bulletins containing the results of fishery research by their own or co-operating scientists. Perhaps the oldest and best known of such publications by maritime States are Fish Bulletins and the serial journal "California Fish and Game" of the California Department of Fish and Game. Also on the Pacific coast, the States of Washington and Oregon have issued their own fishery journals for many years. Several Atlantic coastal States, including Maine, Massachusetts, Maryland, South Carolina, and Florida publish scientific journals or occasional bulletins. A number of inland States also publish scientific fishery journals. In addition, many States publish popular wildlife magazines which contain many articles on fisheries. The great variety of scientific and popular fishery journals in the United States is well illustrated in the Conservation Directory of the National Wildlife Federation (loc cit).

The interstate fishery commissions summarize the results of research in their annual reports. These commissions also issue special scientific reports from time to time. The Pacific Marine Fisheries Commission publishes scientific papers in its annual reports.

Several universities in the United States publish fishery journals. The Gulf and Caribbean Fisheries Institute of the University of Miami publishes proceedings annually. The Institute of Marine Science at the same University publishes the Bulletin of Marine Science of the Gulf and Caribbean. The Natural Resources Institute of the University of Maryland issues the journal Chesapeake Science, which is predominantly a fishery journal. The Institute of Marine Science of the University of Texas publishes a journal at irregular intervals which contains many fishery papers. The University of Indiana issues Investigations of Indiana Lakes and Streams.

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[31] Summary of laws relating to commercial fishing on the Great Lakes. Compiled by the Great Lakes Fishery Commission with the assistance of the Great Lakes States and Ontario. Ann Arbor, Michigan, 44 pp., 1964.

TABLE 13

PUBLICATION SERIES OF THE U.S. FISH AND WILDLIFE SERVICE IN WHICH SCIENTIFIC FISHERY PAPERS OR REPORTS ON THE RESULTS OF RESEARCH APPEAR

	BCF	BSFW
Fishery Bulletins	x	
Special Scientific Reports - Fisheries	x	x
Fishery Industrial Research	x	
Commercial Fisheries Review	x	
Commercial Fisheries Abstracts	x	
Circulars	x	x
Statistical Digests	x	
Fishery Leaflets	x	x
Fishery and Oceanography Translations	x	
Data Reports (on microfiche)	x	
Annual Reports	x	x
Conservation Notes	x	x
Market News Bulletins	x	
Progressive Fish Culturist		x
Research Reports		x
Sport Fisheries Abstracts		x
Market Development Leaflets	x	
Regulatory Announcements	x	x
Separates (reprints from CFR)	x	
Test Kitchen Series	x	
Conservation Backgrounds	x	x

The American Fisheries Society publishes quarterly Transactions. The National Shellfisheries Association issues annual Proceedings. Both serials are of long standing, the former in its 94th year of publication, the latter in its 55th. These are the only private scientific journals in the United States devoted entirely to fishery science. Fishery papers by United States scientists appear in a great many other scientific journals. Federal, State, and university fishery scientists report the results of their research in many journals not issued by their own organizations. Fishery scientists of the Bureau of Commercial Fisheries, for example, publish about two-thirds of all their papers in non-Federal journals, domestic and foreign (Table 14). The best way to obtain a fairly complete listing of journals in which U.S. scientific fishery papers appear would be to scan the lists of literature cited in a representative series of fishery publications. Such a listing would include the proceedings of most of the State academies of science and a wide variety of other journals.

TABLE 14

PUBLICATIONS OTHER THAN FEDERAL GOVERNMENT JOURNALS IN WHICH SCIENTIFIC PAPERS OR ARTICLES WERE PUBLISHED BY EMPLOYEES OF THE BUREAU OF COMMERCIAL FISHERIES IN 1962

Journal or Other Publication	Numbers of Papers
Copeia	17
Transactions of the American Fisheries Society	16
Fish in Nutrition, Proceedings of the FAO World Conference on Fish in Nutrition	8
Chesapeake Science	7
Journal of the Fisheries Research Board of Canada	7
Proceedings of the 1st National Coastal and Shallow Water Research Conference	6
Journal of the Association of Official Agricultural Chemists	5
Journal du Conseil	5
Biological Bulletin	4
Fishing Gazette	4
Food Technology	4
Poultry Science	4
Proceedings of the Gulf and Caribbean Fisheries Institute	4
Proceedings of the World Scientific Meeting on the Biology of Sardines and Related Species	4
The Fish Boat	4
American Naturalist	3
Bulletin of Marine Science of the Gulf and Caribbean	3
Great Lakes Fishery Commission, Technical Reports	3
Journal of the American Oil Chemists Society	3
Limnology and Oceanography	3
Proceedings of the Government-Industry Instrumentation Symposium	3
Proceedings of the National Shellfisheries Association	3

Journal or Other Publication	Numbers of Papers
Annals of the New York Academy of Sciences	2
Atlantic States Marine Fisheries Commission, 21st Annual Meeting	2
Bulletin of the International North Pacific Fisheries Commission	2
California Fish and Game	2
Conseil Permanent International pour l'Exploration de la Mer, Rapports et proces-Verbaux des Reunions	2
Ecology	2
Izaak Walton Magazine	2
Journal of Food Science	2
Journal of Lipid Research	2
Nautilus	2
Pacific Science	2
Proceedings of the 5th Conference on Great Lakes Research	2
Quick Frozen Foods	2
Science	2
The Auk	2
Tulane Studies in Zoology	2
United Nations Conference on the Application of Science and Technology for the Benefit of Less Developed Areas	2
University of British Columbia, H.R. MacMillan Lectures in Fisheries	2
American Biology Teacher	1
American Geographical Society, Serial Atlas of the Marine Environment	1
American Zoologist	1
Applied Microbiology	1
Bulletin of the American Meteorological Society	1
Bulletin of Marine Ecology	1
Bulletin de l'Institut International du Froid	1
Bulletin of the Inter-American Tropical Tuna Commission	1
Bulletin of Zoological Nomenclature	1

	Numbers of Papers
Carlsberg Foundation, Dana Reports	1
Comtes Rendus des seances de l'Academie des Sciences	1
Electronics Magazine	1
FAO Special Publications	1
Feedstuffs	1
Fishing News International	1
Instrumentation (Minneapolis-Honeywell)	1
International Association of Fish Meal Manufacturers, News Summary	1
International Symposium on Microchemical Techniques	1
Journal of Cell Biology	1
Journal of Experimental Medicine	1
Journal of Geophysical Research	1
Journal of Mammalogy	1
Journal of Wildlife Management	1
Maine Field Naturalist	1
Murrelet	1
National and Maine Coast Fisherman	1
National Fur News	1
Pacific Fisherman	1
Proceedings of the Biological Society of Washington	1
Proceedings of the 1st International Conference on Wildlife Disease	1
Proceedings of the 12th Alaska Science Conference	1
Proceedings of the International Commission for the Northwest Atlantic Fisheries	1
Proceedings of the International Institute of Refrigeration	1
Seafood Merchandising	1
The Science Teacher	1
Transactions of the 27th North American Wildlife Conference	1

Journal or Other Publication	Numbers of Papers
Transactions of the Society of Mining Engineers	1
Virginia Journal of Science	1

APPENDIX I

THE INTERSTATE FISHERY COMMISSIONS AND CO-ORDINATION OF FISH AND WILDLIFE ACTIVITIES

Atlantic States Marine Fisheries Commission (16 U.S.C. 667a)

This Resolution authorized the named States to enter into a compact for co-operative effort and mutual assistance for the uniform, common or mutual regulation of fishing in the territorial waters and bays and inlets of the Atlantic Ocean on which such named States border or have jurisdiction. The subsequent interstate compact, as amended, (56 Stat. 267, Public Law 539, 77th Cong., Act of May 4, 1942; 64 Stat. 467, Public Law 721, 81st Cong., Act of August 19, 1950), designated the Fish and Wildlife Service as the primary research agency to promote better utilization of the Atlantic coast fish and shellfish resources.

54 Stat. 261	Public Resolution 79, 76th Cong.	Joint Resolution of June 8, 1940

Pacific Marine Fisheries Commission, Act of July 24, 1947 (61 Stat. 419)

This Resolution authorized the named States (California, Washington, and Oregon) to enter into a compact for co-operative effort and mutual assistance for better utilization of fisheries, marine, shell and anadromous, and to develop a joint program of protection and prevention of physical waste of such fisheries in all of those areas of the Pacific Ocean over which said States jointly or separately have or may acquire jurisdiction.

Amended as follows, Sec. 2, Article XII

"The States of Alaska or Hawaii, or any State having rivers or streams tributary to the Pacific Ocean may become a contracting State by enactment of the Pacific Marine Fisheries Compact. Upon admission of any new State to the compact, the purposes of the compact and the duties of the commission shall extend to the development of joint programs for the conservation, protection and prevention of physical waste of fisheries in which the contracting States are mutually concerned and to all waters of the newly admitted State necessary to develop such program."

76 Stat. 763	Public Law 87-766	87th Congress, S. 3431; HR. 12205 October 9, 1962

Gulf States Marine Fisheries Commission (not codified)

Resolution granting the consent and approval of Congress to an interstate compact relating to the better utilization of the fisheries (marine, shell, and anadromous) of the Gulf coast and creating the Gulf States Marine Fisheries Commission. The compact designates the Fish and Wildlife Service as the primary research agencies of each named State.

63 Stat. 70	Public Law 66, 81st Cong.	Joint Resolution of May 19, 1949

Fish and Wildlife Co-ordination Act, as amended (16 U.S.C. 661-666c)

Authorizes the Secretary of the Interior to co-operate with Federal, State, and public or private agencies in the conservation and development of fish and wildlife resources affected by water-resource development programs. He is further authorized to make reports and recommendations on wildlife aspects of such projects based on surveys and investigations to be conducted by the Fish and Wildlife Service. These reports and recommendations are made an integral part of the report prepared by any Federal agency, responsible for engineering surveys and construction of such projects, to be presented to Congress or authorizing agency.

48 Stat. 401	Public Law 121, 73rd Cong.	Act of March 10, 1934
60 Stat. 1080	Public Law 732, 79th Cong.	Act of August 14, 1946
62 Stat. 497	Public Law 697, 80th Cong.	Act of June 19, 1948
72 Stat. 563	Public Law 85-624	Act of August 12, 1958

APPENDIX II

FISH AND WILDLIFE ACT OF 1956, AS AMENDED 32/
(An Excerpt from Title 16 of the United States Code)

Sec. 742a. Declaration of policy

The Congress declares that the fish, shellfish, and wildlife resources of the Nation make a material contribution to our national economy and food supply, as well as a material contribution to the health, recreation, and well-being of our citizens; that such resources are a living, renewable form of national wealth that is capable of being maintained and greatly increased with proper management, but equally capable of destruction if neglected or unwisely exploited; that such resources afford outdoor recreation throughout the Nation and provide employment, directly or indirectly, to a substantial number of citizens; that the fishing industries strengthen the defense of the United States through the provision of a trained seafaring citizenry and action-ready fleets of seaworthy vessels; that the training and sport afforded by fish and wildlife resources strengthen the national defense by contributing to the general health and physical fitness of millions of citizens; and that properly developed, such fish and wildlife resources are capable of steadily increasing these valuable contributions to the life of the Nation.

The Congress further declares that the fishing industry, in its several branches, can prosper and thus fulfill its proper function in national life only if certain fundamental needs are satisfied by means that are consistent with the public interest and in accord with constitutional functions of governments. Among these needs are:

(1) Freedom of enterprise - freedom to develop new areas, methods, products, and markets in accordance with sound economic principles, as well as freedom from unnecessary administrative or legal restrictions that unreasonably conflict with or ignore economic needs;

(2) Protection of opportunity - maintenance of an economic atmosphere in which domestic production and processing can prosper; protection from subsidized competing products; protection of opportunity to fish on the high seas in accordance with international law;

(3) Assistance - assistance consistent with that provided by the Government for industry generally, such as is involved in promoting good industrial relations, fair trade standards, harmonious labor relations, better health standards and sanitation; and including, but not limited to -

    (a) services to provide current information on production and trade, market promotion and development, and an extension service,

    (b) research services for economic and technologic development and resource conservation, and

    (c) resource management to assure the maximum sustainable production for the fisheries.

32/ Section 1 of the Act of August 8, 1956, provided that the Act, which enacted sections 742a-742d, 742e-742j of Title 16 of the United States Code, and amended section 713c-3(e) of Title 15 of the United States Code, should be popularly known as the "Fish and Wildlife Act of 1956". Section 713c-3 of Title 15 was enacted by the Act of July 1, 1954, which has come to be known as the Saltonstall-Kennedy Act or S-K Act. The text of this latter Act is available in Fishery Leaflet 556.

The Congress further declares that the provisions of sections 742a-742j of this title are necessary in order to accomplish the objective of proper resource development, and that such sections shall be administered with due regard to the inherent right of every citizen and resident of the United States to engage in fishing for his own pleasure, enjoyment, and betterment, and with the intent of maintaining and increasing the public opportunities for recreational use of our fish and wildlife resources, and stimulating the development of a strong, prosperous, and thriving fishery and fish processing industry. (Aug. 8, 1956, ch. 1036, Sec. 2, 70 Stat. 1119)

Sec. 742b. United States Fish and Wildlife Service.

(a) Establishment; Assistant Secretary for Fish and Wildlife and Commissioner of Fish and Wildlife; Bureau of Commercial Fisheries and Bureau of Sport Fisheries and Wildlife.

There is established within the Department of the Interior the position of Assistant Secretary for Fish and Wildlife, and the position of Commissioner of Fish and Wildlife. Such Assistant Secretary shall be appointed by the President, by and with the advice and consent of the Senate, and shall be compensated at the same rate as other Assistant Secretaries. The Commissioner shall be appointed by the President by and with the advice and consent of the Senate. There is also established a United States Fish and Wildlife Service within the Department, consisting of two separate agencies, each of which shall have the status of a Federal bureau. There shall be a Director of each of said Bureaux appointed by the Secretary. One of the agencies shall be known as the "Bureau of Commercial Fisheries" and the other agency shall be known as the "Bureau of Sport Fisheries and Wildlife". The United States Fish and Wildlife Service, except as prescribed by sections 742a-742j of this title, shall succeed to and replace the presently existing Fish and Wildlife Service of the Department.

(b) Administration and supervision.

The functions of the United States Fish and Wildlife Service hereby established shall be administered under the supervision of the said Commissioner of Fish and Wildlife, who shall be subject to the supervision of the Assistant Secretary for Fish and Wildlife.

(c) Functions and responsibilities of Secretary of the Interior.

All functions and responsibilities placed in the Department of the Interior or any official thereof by sections 742a-742j of this title shall be included among the functions and responsibilities of the Secretary of the Interior, as the head of the Department, and shall be carried out under his direction pursuant to such procedures or delegations of authority as he may deem advisable and in the public interest.

(d) Distribution of functions, powers and duties of former Fish and Wildlife Service.

In order to make a proper distribution between the two Bureaux of the United States Fish and Wildlife Service established by sections 742a-742j of this title, the previously existing functions, powers, duties, authority, liabilities, commitments, personnel, records, and other properties or matters previously handled by or administered through the former Fish and Wildlife Service of the Department, shall be distributed as follows:

(1) The Bureau of Commercial Fisheries shall be responsible for those matters to which sections 742a-742j of this title apply relating primarily to commercial fisheries, whales, seals, and sea-lions, and related matters;

(2) The Bureau of Sport Fisheries and Wildlife shall be responsible for those matters to which sections 742a–742j of this title apply relating primarily to migratory birds, game management, wildlife refuges, sport fisheries, sea mammals (except whales, seals and sea-lions), and related matters; and the funds and allocations, appropriated or otherwise, relating to the matters covered by paragraphs (1) and (2) of this subsection shall be distributed between such Bureaux as the Secretary of the Interior shall determine.

(e) Rules and regulations.

Except as changed by the terms of sections 742a–742j of this title or by subsequent laws or regulations, all laws and regulations now in effect relating to matters heretofore administered by the Department of the Interior through the former Fish and Wildlife Service as heretofore existing, shall remain in effect.

(f) Administrative procedures.

In recognition of the need for authority to execute the purposes of sections 742a–742j of this title effectively, the Secretary of the Interior shall exercise such general administrative authority consistently with the terms of such sections as he shall find to be necessary to carry out the provisions of such sections effectively and in the public interest. In order to allow sufficient time to place the reorganizations under such sections into effect, the Secretary is authorized to establish an effective procedure and date of such reorganizations, notice of which shall be published in the Federal Register. Such reorganization shall be accomplished as soon as practicable after August 8, 1956, but not later than ninety (90) calendar days after August 8, 1956. (Aug. 8, 1956, ch. 1036, Sec. 3, 70 Stat. 1120; Oct. 4, 1961, Pub. L. 87-367, title I, Sec. 103(14), 75 Stat. 788; Oct. 11, 1962, Pub. L. 87-793, Sec. 607(a)(5), 76 Stat. 849.)

/Amendments/

/1962 – Subsec. (a). Pub. L. 87-793 eliminated provisions which authorized the Commissioner to receive compensation at the same rate as that provided for grade GS-18./
/1961 – Subsec. (a). Pub. L. 87-367 deleted "at Grades GS-17 each" following "by the Secretary"./

Sec. 742c. Loans for financing and refinancing of operations, maintenance, replacement, repair, and equipment of fishing gear, and vessels, and for research.

(a) Authorization.

The Secretary is authorized under rules and regulations and under terms and conditions prescribed by him, to make loans for financing and refinancing of operations, maintenance, replacement, repair, and equipment of fishing gear and vessels, and for research into the basic problems of fisheries.

(b) Conditions.

Any loans made under the provisions of this section shall be subject to the following restrictions:

(1) Bear an interest rate of not less than 3 per centum per annum;

(2) Mature in not more than ten years;

(3) No financial assistance shall be extended pursuant to this section unless reasonable financial assistance applied for is not otherwise available on reasonable financial assistance applied for is not otherwise available on reasonable terms.

(c) Fisheries loan fund.

There is created a fisheries loan fund, which shall be used by the Secretary as a revolving fund to make loans for financing and refinancing under this section. Any funds received by the Secretary on or before June 30, 1965, in payment of principal or interest on any loans so made, shall be deposited in the fund and be available for making additional loans under this section. Any funds so received after June 30, 1965 and any balance remaining in the fund at the close of June 30, 1965 (at which time the fund shall cease to exist), shall be covered into the Treasury as miscellaneous receipts. There are authorized to be appropriated to the fund the sum of $20,000,000 to provide initial capital.

(d) Modification of loan contract.

The Secretary, subject to the specific limitations in this section, may consent to the modification, with respect to the rate of interest, time of payment of any instalment of principal, or security, of any loan contract to which he is a party. (Aug. 8, 1956, ch. 1036, Sec. 4, 70 Stat. 1121; Sept. 2, 1958, Pub. L. 85-888, 72 Stat. 1710.)

/Amendments/

/1958 - Subsec. (c) amended by Pub. L. 85-888 to increase authorization for $10,000,000 to $20,000,000./

Sec. 742d. Investigations; preparation and dissemination of information; reports.

The Secretary shall conduct continuing investigations, prepare and disseminate information, and make periodical reports to the public, to the President, and to Congress, with respect to the following matters:

(1) The production and flow to market of fish and fishery products domestically produced, and also those produced by foreign producers which affect the domestic fisheries;

(2) The availability and abundance and the biological requirements of the fish and wildlife resources;

(3) The competitive economic position of the various fish and fishery products with respect to each other, and with respect to competitive domestic and foreign-produced commodities;

(4) The collection and dissemination of statistics on commercial and sport fishing;

(5) The collection and dissemination of statistics on the nature and availability of wildlife, progress in acquisition of additional refuges and measures being taken to foster a co-ordinated program to encourage and develop wildlife values;

(6) The improvement of production and marketing practices in regard to commercial species and the conduct of educational and extension services relative to commercial and sport fishing, and wildlife matters;

(7) Any other matters which in the judgment of the Secretary are of public interest in connection with any phases of fish and wildlife operations.

(Aug. 8, 1956, ch. 1036, Sec. 5, 70 Stat. 1121.)

Sec. 742e. Transfer of functions, personnel, property, facilities, records, and funds; co-operation with other governmental agencies.

(a) There shall be transferred to the Secretary all functions of the Secretary of Agriculture, the Secretary of Commerce, and the head of any other department or agency, as determined by the Director of the Bureau of the Budget to relate primarily to the development, advancement, management, conservation, and protection of commercial fisheries; but nothing in this section shall be construed to modify the authority of the Department of State or the Secretary of State to negotiate or enter into any international agreements, or conventions with respect to the development, management, or protection of any fisheries and wildlife resources or with respect to international commissions operating under conventions to which the United States is a party.

(b) There shall be transferred to the Department of the Interior so much of the personnel, property, facilities, records, and unexpended balances of appropriations, allocations, and other funds (available or to be made available) as the Director of the Bureau of the Budget determines to be necessary in connection with the exercise of any functions transferred to the Secretary pursuant to subsection (a) of this section.

(c) The Secretary may request and secure the advice or assistance of any department or agency of the Government in carrying out the provisions of sections 742a-742j of this title, and any such department or agency which furnishes advice or assistance to the Secretary may expend its own funds for such purposes, with or without reimbursement from the Secretary as may be agreed upon between the Secretary and the department or agency. (Aug. 8, 1956, ch. 1036, Sec. 6, 70 Stat. 1122.)

Sec. 742f. Policies, procedures, and recommendations.

(a) The Secretary of the Interior, with such advice and assistance as he may require from the Assistant Secretary for Fish and Wildlife, shall consider and determine the policies and procedures that are necessary and desirable in carrying out efficiently and in the public interest the laws relating to fish and wildlife. The Secretary, with the assistance of the departmental staff herein authorized, shall -

(1) develop and recommend measures which are appropriate to assure the maximum sustainable production of fish and fishery products and to prevent unnecessary and excessive fluctuations in such production;

(2) Study the economic condition of the industry, and whenever he determines that any segment of the domestic fisheries has been seriously disturbed either by wide fluctuation in the abundance of the resource supporting it, or by unstable market or fishing conditions or due to any other factors he shall make such recommendations to the President and the Congress as he deems appropriate to aid in stabilizing the domestic fisheries.

(3) develop and recommend special promotional and informational activities with a view to stimulating the consumption of fishery products whenever he determines that there is a prospective or actual surplus of such products;

(4) take such steps as may be required for the development, advancement, management, conservation, and protection of the fisheries resources; and

(5) take such steps as may be required for the development, management, advancement, conservation, and protection of wildlife resources through research, acquisition of refuge lands, development of existing facilities, and other means.

(Aug. 8, 1956, ch. 1036, Sec. 7, 70 Stat. 1122)

[Codification]

[Section was enacted without a subsection (b).]

(a) The Secretary shall co-operate to the fullest practicable extent with the Secretary of State in providing representation at all meetings and conferences relating to fish and wildlife in which representatives of the United States and foreign countries participate.

The Secretary of State shall designate the Secretary of the Interior or the Assistant Secretary for Fish and Wildlife, or a person designated by the Secretary of the Interior to represent the Department of the Interior, as a member of the United States delegation attending such meetings and conferences and also as a member of the negotiating team of any such delegation.

(b) The Secretary of State and all other officials having responsibilities in the fields of technical and economic aid to foreign nations shall consult with the Secretary in all cases in which the interests of fish and wildlife are involved, with a view to assuring that such interests are adequately represented at all times.

(c) Notwithstanding any other provision of law, the Secretary shall be represented in all international negotiations conducted by the United States pursuant to section 1351 of Title 19, in any case in which fish products are directly affected by such negotiations.

(d) The Secretary shall consult periodically with the various governmental, private nonprofit, and other organizations and agencies which have to do with any phase of fish and wildlife with respect to any problems that may arise in connection with such fish and wildlife.
(Aug. 8, 1956, ch. 1036, Sec. 8, 70 Stat. 1123.)

Sec. 742h. Reports to Congress and the President.

(a) The Secretary of the Interior shall make an annual report to the Congress with respect to activities of the United States Fish and Wildlife Service under section 742a-742j of this title, and shall make such recommendations for additional legislation as he deems necessary.

(b) The Secretary is authorized to make a report to the Presient and the Congress, and, when requested by the United States Tariff Commission in connection with section 1364 of Title 19, or when an investigation is made under the Tariff Act of 1930, the Secretary is authorized to make a report to such Commission, concerning the following matters with respect to any fishery product which is imported into the United States, or such reports may be made upon a request from any segment of the domestic industry producing a like or directly competitive product -

(1) whether there has been a downward trend in the production, employment in the production, or prices, or a decline in the sales, of the like or directly competitive product by the domestic industry; and

(2) whether there has been an increase in the imports of the fishery products into the United States, either actualy or relative to the production of the like or directly competitive product produced by the domestic industry.

(Aug. 8, 1956, ch. 1036, Sec. 9, 70 Stat. 1123.)

Sec. 742i. Effect on rights of States and international commissions.

Nothing in sections 742a-742j of this title shall be construed (1) to interfere in any manner with the rights of any State under the Submerged Lands Act or otherwise provided by law, or to supersede any regulatory authority over fisheries exercised by the States either individually or under interstate compacts; or (2) to interfere in any manner with the authority exercised by any International Commission established under any treaty or convention to which the United States is a party. (Aug. 8, 1956, ch. 1036, Sec. 10, 70 Stat. 1124.)

Sec. 742j. Appropriations.

There are authorized to be appropriated such sums as may be necessary to carry out the provisions of sections 742a-742j of this title. (Aug. 8, 1956, ch. 1036, Sec. 11, 70 Stat. 1124.)

Sec. 742k. [33] Management and disposition of vessels and other property acquired and arising out of fishery loans or related type of activities.

For the purpose of facilitating administration of, and protecting the interest of the Government in, the fishery loan fund established by section 742c of this title and any related type of activities relating to fisheries for which the Department of the Interior is now or may hereafter be responsible, the Secretary of the Interior, notwithstanding any other provision of law, may hereafter administer, complete, recondition, reconstruct, renovate, repair, maintain, operate, charter, assign, or sell upon such terms and conditions as he may deem most advantageous to the United States, any vessel, plant, or other property acquired by him or on behalf of the United States and arising out of any fishery loan or any related type of activity by the Secretary of the Interior. The Secretary may use any of the applicable funds in each particular instance for the aforesaid purposes. (Sept. 13, 1961, Pub. L. 87-219, 75 Stat. 493.)

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[33] This section was not enacted as a part of the Fish and Wildlife Act of 1956 nor as an amendment to it. The section pertains to section 4 of the Fish and Wildlife Act of 1956, however, and is codified with it.

Family Aulopidae

GILES W. MEAD
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Acknowledgments. Many individuals have contributed substantially to the work on the Aulopidae, Chlorophthalmidae (p. 162), Bathypteroidae (p. 114), Ipnopidae (p. 147), and Bathysauridae (p. 103). My thanks are due those who have provided study specimens: Loren P. Woods and the late Mrs. Marion Grey, Chicago Natural History Museum; George S. Myers and the late Miss Margaret H. Storey, Division of Systematic Biology, Stanford University; James E. Morrow, Jr., formerly of the Bingham Oceanographic Laboratory, Yale University; C. Richard Robins, Marine Laboratory, University of Miami; Royal D. Suttkus, Tulane University; William C. Schroeder and Mrs. Myvanwy Dick, Museum of Comparative Zoology, Harvard University; Leonard P. Schultz and Ernest A. Lachner, United States National Museum; G. E. Maul, Museu Municipal do Funchal, Madeira; Enrico Tortonese, Museum of Natural History, Genoa; and Max Poll, Musée Royal du Congo Belge, Tervuren. I am also indebted to N. B. Marshall of the British Museum (Natural History) for re-examining for me the type specimens of Bathypterois quadrifilis, Bathysaurus ferox, *and* Bathytyphlops sewelli, *and to Einar Koefoed of the Bureau of Fisheries, Bergen, Norway, for needed information from* Michael Sars *specimens of* Bathysaurus.

When this study was begun, several biologists aboard the exploratory vessels of the United States Fish and Wildlife Service collected large series of specimens and data for my use. I wish here to record my appreciation to Stewart Springer, Harvey R. Bullis, Jr., Warren F. Rathjen, William W. Anderson, Jack W. Gehringer, Frederick H. Berry, David K. Caldwell, and all of the U.S. Fish and Wildlife Service.

Reprinted from Memoir Sears Foundation for Marine Research, I (5), 1966: 19–29.

Characters. MODERATELY SLENDER BOTTOM FISHES OF THE CONTINENTAL SHELF THAT ATTAIN A LENGTH OF ABOUT TWO FEET. Body compressed posteriorly, nearly circular in cross section anteriorly. Snout rounded. Eye of moderate size, approximately round and laterally directed. Pupil round (*vs.* elliptical or keyhole-shaped as in many families such as the Chlorophthalmidae); no aphakic (lensless) space. Interorbital space broad and slightly concave; circumorbital bones conspicuous and well ossified; the large supraorbital fused to the skull.

Scales present on cheeks, gill covers, body, and base of caudal fin, the scales adherent and ctenoid or cycloid; scales on operculum notably larger than those elsewhere; top of head naked. Lateral line well developed, not extending onto caudal fin but terminating over base of central caudal fin ray.

Dorsal fin anterior, its origin in first third of body; its base, in Atlantic species, shorter than length of head, but shorter or longer than head in Pacific species; the fin composed of about 14–21 rays. Anal fin originating in posterior half of body and composed of 9–13 rays. Caudal fin forked, the lobes approximately equal in length, the fin with 19 (I-17-I) principal rays. Ventral fins thoracic, located approximately under origin of dorsal fin and composed of 9 rays, lying in an oblique plane when expanded, the rays frequently with thickened tips. Pectoral fin inserted laterally, undivided (*cf.* Bathypteroidae), without prolonged rays, and containing 11–14 rays. Dorsal adipose fin well developed, situated over posterior end of base of anal fin.

Anus closer to origin of anal fin than to insertion of ventral fin. A minute anal papilla present.

No luminous organs.

Lower jaw usually terminal, but coterminal with upper in some Pacific forms. Upper jaw extending to or beyond middle of eye. Both maxillary and premaxillary well developed, the maxillary excluded from the gape. Maxillary dilated behind. Two well-developed supramaxillary bones.

Tongue well developed and free from the floor of the mouth, supported by a well-developed and horizontal glossohyal bone.

Teeth present on jaws, vomer, palatines, and tongue; numerous, mostly depressible, recurved and needle-like, some with slight barb-like expansions at the tip. No enlarged canine or lanceolate teeth (*cf.* the fixed vomerine fangs of *Parasudis* which are notably longer than the other teeth, or the depressible vomerine series of some of the alepisauroid fishes).

Gill arches not extending farther forward into the mouth than angle of gape. Gill rakers of the normal lath-like shape. Pseudobranchiae well developed and not covered by skin. Branchiostegal membranes broadly overlapping across isthmus and covered by a heavy gular fold; not extending posteriorly beyond opercular flap. About 16 branchiostegal rays, half of them inserted on the epihyal, half on the ceratohyal. Opercular flap well ossified, the opercular bone excluded from the free posterior edge of the opercular flap by a dorsal extension of the subopercle.

Dioecious. Vertebrae 41–53.[1]

Many of the species show prominent sexual differences[2] in the height of the unpaired fins, particularly the anterior part of the dorsal. In the males, the second and third rays are prolonged, and all dorsal and anal rays are somewhat longer.

Development. Except for limited information on the development of *A. filamentosus* in the Mediterranean, nothing is known of the life history of any aulopid species. Sanzo[3] and Tåning (*28*) have described juveniles of *A. filamentosus* of 6.8 to 43.5 mm length—transparent creatures with large fan-shaped pectoral fins and depressed snouts. These young were pelagic. The mature ovarian eggs, 1.36 to 1.44 mm in diameter, contained numerous oil globules. These eggs were taken from females caught near Messina, Italy, during late spring; Sanzo has suggested that the period of sexual maturity may last for many months if not throughout the entire year (*25*).

Relation to Man. A. purpurissatus, the "Sergeant Baker" of Australia, has a wide distribution along the more temperate parts of the Australian coast, where it is normally found on or adjacent to rocky reefs in moderately deep water offshore. It is occasionally caught by sportsmen and by trawl or line fishermen. The young are occasionally found in brackish water.[4]

Elsewhere in the western Pacific, *A. japonicus* is landed and sold for human consumption when caught,[5] but nowhere is the catch sufficiently large or dependable to warrant inclusion in fishery landings statistics or to be of any significant economic importance.

The eastern Atlantic *A. filamentosus* is marketed, but its occurrence is sporadic and its capture incidental to the fishery for other species.[6] It is said to be tasty. The

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[1] Regan (*18*) has described the skull and the pectoral and pelvic girdles of *Aulopus filamentosus*. Since his osteological characterization of the Aulopidae included only this species and not some of those that are quite different, at least externally (for example, *A. japonicus*), his diagnosis may not reflect the true characters of the family as a whole. He has noted that:

"The skeleton of *Aulopus* is well ossified; the skull is rather elongate, without crests on the flattish upper surface, which is nearly at right angles to the posterior surface. The parietals meet above the supraoccipitals and with the pterotics roof the posterior temporal fossae; the cranium broadens out behind the orbits and the sphenotic has a prominent process directed outwards and downwards; the subtemporal fossa is moderately deep; the orbitosphenoid is a vertical lamina extending from the frontals to the parasphenoid and forming a septum in the anterior half of the interorbital region; posteriorly it is separated from the alisphenoids by a pair of inferior ridges of the frontals; the parasphenoid widens out anteriorly on each side into a broad lamina which unites with the lower edge of the lateral ethmoid; the latter is well ossified, but is separated from its fellow by a wide interspace; the mesethmoid appears as a large plate overlying the vomer and has a lateral process on each side supporting an upwardly directed process of the anterior part of the palatine, in front of which that bone is suturally united with the vomer; the well-developed mesopterygoid overlaps the parasphenoid; the series of circumorbitals is noteworthy for the firm attachment of the supraorbital to the lateral ethmoid and frontal and of the uppermost postorbital to the frontal and sphenotic; there is a well developed infranasal; the opercular bones are remarkable for the great development of the suboperculum, which forms the entire posterior margin of the gill-opening; the branchiostegals also are long and curved upwards." The osteology of *A. filamentosus* has also been discussed by Vrolik (*30*), Gregory (*8*), and Woodward (*33*).

[2] This difference is found in *A. filamentosus* and *A. purpurissatus*. The anterior dorsal rays are not prolonged in *A. cadenati* or in *A. nanae*. Sexual dimorphism in *A. japonicus* and *A. damasi* has not been reported.

[3] Sanzo (*23, 24, 25*). In these papers Sanzo has referred the juvenile described as *Pelopsia sicillae* by Facciolà (*7*) to *Aulopus filamentosus*. *P. sicillae* was included in the synonymy of *Chlorophthalmus agassizi* by Parr (*16*).

[4] Roughley (*22*: 12; pl. 2, in color).

[5] Okada (*15*).

[6] For additional data on *A. filamentosus*, see Cuvier and Valenciennes (*5*), Steindachner (*26*), Moreau (*14*), Griffini (*9*), Maul (*13*), L. L. Rey (*11*), Dieuzeide, *et al.* (*6*), and O. G. Costa (*4*).
For a discussion of fossil forms (*Sardinioides*) related to *Aulopus*, see Woodward (*32, 33*).

West African *A. cadenati* appears to be fairly abundant, but there is no fishery operating off tropical Africa in depths frequented by this species and it is unlikely that it will ever be of much commercial importance.

Distribution. The family includes about eight species which are caught on the bottom at moderate depths in tropical and warm-temperate latitudes. Aulopids are common in the western Pacific and eastern Atlantic, unknown from the eastern Pacific, and represented in the western North Atlantic by a species known only from four specimens.

Genera. Three aulopid generic names are in current use: *Aulopus* Cloquet 1816, *Hime* Starks 1924, and *Latropiscis* Whitley 1931. Neither *Hime* nor *Latropiscis* was well defined by its original author. *Hime* was separated from *Aulopus* only by its lack of ossification in the anterior interorbital region ("orbitosphenoid lacking"), while Whitley provided no diagnosis whatsoever for *Latropiscis* but referred only to Cuvier and Valenciennes' account of *A. milesi* and *A. filamentosus*; he did not consider the other Pacific species.

The separation of *Hime* from *Aulopus* on the basis of the orbitosphenoid is a tenuous one. The orbitosphenoid in *A. japonicus* differs from that of *A. filamentosus* or *A. purpurissatus* only in the degree of ossification and in its posterior extent. This bone in *A. japonicus* is very poorly ossified (therefore probably missing from Starks' study skeleton) and restricted to the anterior third of the interocular septum. In the other species that I have examined, this bone is well ossified and occupies approximately the anterior two-thirds of the interocular region. There are, however, other features that characterize *A. japonicus*, for it is a very distinctive fish. Most of these can be attributed to its relatively shorter head and body. It can be distinguished from its congeners by its small number of vertebrae (41) and longitudinal scale rows (about 35) and by its shorter snout and jaws. It can also be separated by dentition (numerous teeth near the edge of the tongue in contrast to median longitudinal patches), and by the shape of the eye, which is more nearly circular than that of *A. filamentosus* although similar in shape to that of *A. purpurissatus*. *A. damasi* was said by its describer to resemble closely its Japanese congener, *A. japonicus*, although the published illustrations of *A. damasi* represent a fish intermediate between *A. japonicus* and *A. purpurissatus* in head proportions if not in fin length and height.

The differences between *A. purpurissatus* and *A. filamentosus* hardly justify generic separation (number of rays in the vertical fins and correlated lengths of fin bases, form of lingual dentition, size of eye, and so on); thus the genus *Latropiscis* cannot be retained.

All of the aulopid species are here included within the single genus *Aulopus*.

Genus *Aulopus* Cloquet 1816

Aulopus Cloquet, Dict. Scien. nat., *3*, 1816: 128; type species, by monotypy, *Aulopus filamentosus* Cloquet 1816. Mediterranean.

Generic Synonyms:

Hime Starks, Copeia, 127, 1924: 30; type species, by original designation, *Aulopus japonicus* Günther, Rep. sci. Res. CHALLENGER, Zool., *1* (6), 1880: 72. Off Japan.

Latropiscis Whitley, Aust. Zool., 6 (4), 1931: 312; type species, by original designation, *Aulopus milesi* Cuvier and Valenciennes, Hist. Nat. Poiss., *22*, 1849: 521; roy. ed. p. 385, pl. 650. Australia.

Characters. Those of the family (p. 20).

Key to Species

1a. Base of dorsal fin much longer than distance from rear end of base of dorsal fin to origin of adipose fin. Pacific species.

  2a. Base of anal fin longer than distance from rear end of base of anal fin to base of most anterior ventral caudal ray; more than 18 dorsal fin rays.[7]
  purpurissatus Richardson 1843.
  Australia.
  milesi Cuvier and Valenciennes 1849.
  Australia.

  2b. Base of anal fin shorter than distance from rear end of base of anal fin to base of most anterior ventral caudal ray; fewer than 18 dorsal fin rays.[8]

    3a. Diameter of orbit equal to or greater than length of snout; about 43 scales in lateral line. *japonicus* Günther 1880.
    Japan, Philippines.

    3b. Diameter of orbit less than length of snout; about 35 scales in lateral line. *damasi* Tanaka 1915.
    Japan.

1b. Base of dorsal fin shorter than distance between rear end of base of dorsal fin and origin of adipose fin. Atlantic species.

  4a. Predorsal scales 15 or 16 (along dorsal midline); about 52 scales in lateral line; anterior dorsal rays of male prolonged into filaments; vertebrae 51, including the hypural.[9] *filamentosus* Cloquet 1816.
  Mediterranean and eastern Atlantic.

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[7] I have but one Australian specimen, a large individual labeled *Aulopus purpurissatus* from southern Australia which was sent to the U.S. National Museum by the Australian Museum (USNM 47915). Therefore I have had to rely on the type accounts of *A. milesi* by Cuvier and Valenciennes (5: 521) and of *A. purpurissatus* by Richardson (*19*). Whitley (*31*) has noted only that "the 'Sergeant Baker' of New South Wales (*Latropiscis milesi*) differs in coloration from the western Australian species (*Latropiscis purpurissatus*) described by Richardson . . .", although there appear to be other differences between the type accounts of the two forms (*e.g.* dorsal fin-ray count). Because of this uncertainty and the lack of specimens, no attempt is made here to distinguish these two Australian species.

[8] The characters used for the separation of the Japanese *A. japonicus* Günther (*10*) from *A. damasi* Tanaka (*27*) are based on Philippine and Japanese specimens of *A. japonicus* (USNM 51422, 135569) and on the key published by Matsubara (*12*) (kindly translated for me from the Japanese by Mr. W. G. van Campen, U.S. Fish and Wildlife Service, Honolulu). I have not seen *A. damasi*, but Tanaka's figure resembles the Australian *A. purpurissatus* more closely than it does *A. japonicus*.

[9] The eastern North Atlantic and Mediterranean form is here referred to *A. filamentosus* Cloquet (*3*). I have compared specimens from Madeira, the Azores and the Mediterranean Sea with accounts of *A. filamentosus* and its supposed synonyms: (?) *A. tirus* (Rafinesque, *17*), *A. lacerta* (Risso, *21*), *A. filifer* and *A. maculatus* (Valenciennes, *29*). It is probable that there are more than one species of eastern North Atlantic *Aulopus*, but a further study of this problem cannot be attempted here. *A. lacerta* (Risso) was based on the *Osmerus saurus* of Risso (*20*). This description

4b. Predorsal scales 12 or 13; 48–51 scales in lateral line; anterior dorsal rays of male not greatly prolonged; vertebrae 48–50, including the hypural.

  5a. Lateral-line scales 50 or 51; penultimate anal fin ray 6–8 % of SL, shorter than depth of body at origin of anal fin (both sexes). *cadenati* Poll 1953.
  Tropical West Africa.

  5b. Lateral-line scales 48; penultimate anal fin ray (of male[10]) more than 15% of SL, much longer than depth of body at origin of anal fin.
  nanae Mead 1958, below.

Aulopus nanae Mead 1958

Figure 7

Study Material. A 223.0-mm male, holotype of the species, caught in the Gulf of Mexico off Tortugas, Florida, at OREGON St. 1025, 25°12′N, 84°05′W, 75 fms., April 19, 1954, 40-foot shrimp trawl, USNM 158985.

Distinctive Characters. Similar to the eastern Atlantic *A. cadenati* and *A. filamentosus* but differing from these principally in the number of predorsal scales (12 *cf.* 13 to 16), the number of vertebrae (48 including the hypural *cf.* 50 to 52), the width of the bony interorbital (3.6 % of SL *cf.* 3.8 to 4.8 %), the length of the ventral fin (27.6 % *cf.* 19.6 to 25.6 %), and the length of the anal fin, the last ray of which is much longer than the depth of the fish measured at the origin of the anal fin (15.2 % of SL *cf.* 7.6 to 9.6 %).

Description. Proportional dimensions in per cent of standard length, from the type specimen referred to above, 223 mm SL.

Body: depth at origin of dorsal fin 16.6; of anal fin 11.7; of adipose fin 9.4; width at base of pectoral fin 15.0.

Caudal peduncle: least depth 6.6.

Head: greatest length 30.0; snout to uppermost point of gill opening 20.6; posterior edge of orbit to uppermost point of gill opening 5.6.

Snout: length 8.3.

Eye: horizontal diameter 6.9; vertical diameter 6.3.

Interorbital: width of bony space 3.6.

Postorbital: length 15.8.

Premaxillary: length 14.6.

Dorsal fin: length of base 21.7; length of penultimate ray 18.6.

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may be that of an aulopid, but he refers to Bloch's pl. 384, fig. 1 (*2*), which appears to be a synodontid. Bertin and Estève (*1*) have designated a dried Risso specimen as the type of *Osmerus saurus* and have included both *saurus* and *lacerta* in the synonymy of *Aulopus filamentosus* in the belief that *filamentosus* was first named by Bloch in 1791. The true identity of Risso's *Osmerus saurus* and *Saurus lacerta* cannot be determined without a re-examination of the original specimens. Both Risso's name *saurus* and Rafinesque's *tirus* predate *filamentosus*.

[10] The type of *Aulopus nanae* is a male. The anal fin of this specimen is much higher than that of male eastern Atlantic *A. filamentosus* and *A. cadenati*, but the fin of female *A. cadenati* is considerably lower. Three additional specimens have been caught: a 171-mm male, in which the penultimate anal ray is about 10.2% of SL, a 178-mm female with this ray 7.9% as long as the fish, and a 181-mm female in which this ratio is 8.0. It appears, then, that the rear fin rays of the male *A. nanae* are considerably longer than those of the female.

Anal fin: length of base 13.9; height when depressed 29.1; length of second ray 12.8; of penultimate ray 16.6; of last ray 15.2.

Ventral fin: length 27.6.

Distance from snout to origin of: dorsal fin 36.4; anal fin 68.8; pectoral fin 29.6; ventral fin 34.9.

Distance from origin of anal fin to: origin of dorsal fin 38.3; origin of ventral fin 35.6; end of base of dorsal fin 18.8; anus 10.5.

Scales: in lateral line 48; predorsal 12.

Branchiostegal rays: 15 or 16.

Gill rakers: on first arch 3 + 1 + 10.

Fin rays: dorsal 15; caudal 1-17-1; anal 12; pectoral 12 or 13; ventral 9.

Vertebrae: 47 + 1.

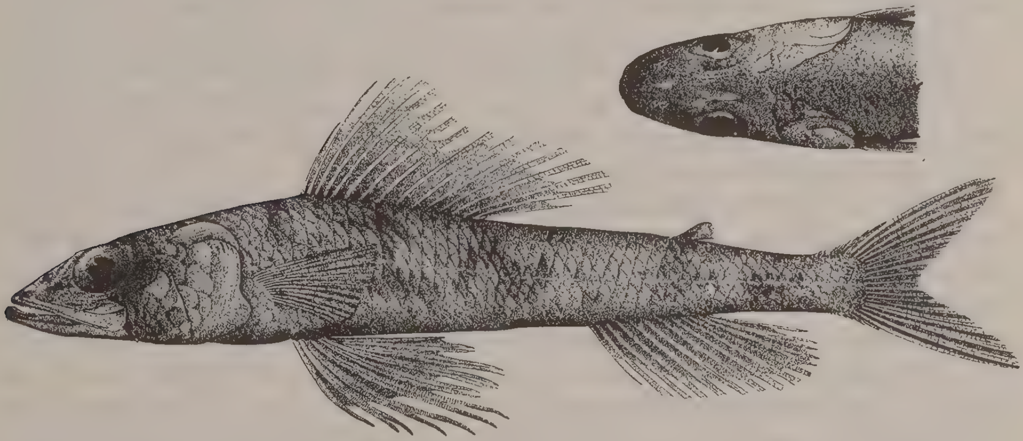

FIGURE 7. *Aulopus nanae,* 223 mm long, OREGON St. 1025, Gulf of Mexico off Tortugas, Florida, 75 fms., USNM 158985, holotype. Drawn by Nancy W. Mead.

BODY subcylindrical, broadest at origin of pectoral fin; and snout depressed; the ventral profile nearly straight from tip of lower jaw to caudal peduncle; the body deepest at origin of dorsal fin, the depth at this point 1.8 in hl; depth at origin of anal fin 2.6 in hl. Least depth of CAUDAL PEDUNCLE 4.5 in hl. SCALES present on cheeks, opercles, body, and base of caudal fin; top of head, snout and mandible naked; scales on head and sides of body with saw-like serrations, those on ventral surface with smooth edges, the body scales relatively large and imbricate, the cteni numerous and irregular in size; scales in axil of pectoral fin lacking cteni and more closely imbricate than body scales but of similar size and shape; scales in axil of pelvic fin vertically elongate but not greatly enlarged. LATERAL LINE complete, terminating over base of midcaudal ray, each of its scales bearing a simple tube, but otherwise similar to the scales adjacent to the lateral line.

Length of HEAD 3.3 in SL. Length of SNOUT 3.6 in hl, the lower jaw terminal. EYE irregularly circular, entering into dorsal profile, its horizontal diameter 4.3 in hl.

Iris round. Horizontal diameter of Orbit greater than the vertical, a notch along lower edge of orbit. Width of Fleshy interorbital space slightly greater than vertical diameter of eye. Width of Bony interorbital space 1.9 in horizontal diameter of eye. Nostril located about 67 % of distance from tip of snout to anterior edge of orbit. Septum between anterior and posterior nostril with a simple cirrus, the length of which is about half the width of the bony interorbital space. Opercular flap long and thin, extending posteriorly below and beyond origin of pectoral fin, the posterior edge formed by the subopercle.

Gill rakers present on 1st and 2nd arches; those on the 1st arch bearing spines of moderate length along the inner side and at the tip, the raker at the angle about the same length as the opposing gill filament; those on the 2nd arch covered with spines throughout. On the 3rd and 4th arches, patches of spines on the arches themselves, replacing the rakers.

Upper jaw bones (maxillary and premaxillary) extending to below posterior fourth of eye, the length 2.1 in hl, expanded posteriorly, and bearing two supramaxillaries, the larger overlying the posterior half of the maxillary. Angle of gape below center of eye. Anterior and lateral surfaces of Lower jaw rugose.

Teeth present on mandible, tongue and premaxillary, vomer, and palatine bones; symphysis of lower jaw without teeth. Rami with a broad band of pointed, conical teeth, straight or slightly recurved, the inner teeth of this band longer than the outer and depressible. Most of the larger outer mandibular teeth depressible, the smaller ones fixed. A broad longitudinal band of minute teeth on tongue. Teeth on premaxillary in a broad band similar to those on the mandible; the inner ones largest, conical and pointed, slightly recurved and depressible; the center ones smaller, with some larger depressible teeth and a greater number of smaller fixed teeth. A patch of depressible teeth of various sizes on the vomer; the vomerine dentition continuous across the roof of the mouth anteriorly. Two rows of conical teeth on each palatine, the inner teeth longer and more easily depressible than the outer.[11]

Dorsal fin long and high,[12] the length of penultimate ray 1.2 in length of base, the anterior 2 rays simple, the distance from snout to origin 2.8 in SL. Adipose fin inserted over 6th anal ray, its length equal to width of base of ventral fin. Anal fin with length of base 2.2 in hl, its height (from insertion to tip when depressed) almost equal to hl; distance from snout to origin of anal fin 1.5 in SL, from end of base of dorsal fin to origin of anal fin 5.3 in SL, and from anus to origin of anal fin 2.8 in hl; the length of penultimate ray much greater than depth of body at origin of fin, 1.8 in hl. Pectoral fin extending to beneath base of 7th dorsal ray, the upper 2 rays simple and the remainder branched, the distance from snout to insertion 3.4 in SL. Ventral fin 1.1 in hl, extending beyond anus, the first and last rays simple but the rest branched, the ends of the anterior 4 rays thickened, the distance from snout to origin of ventral fin 2.9 in SL and about equal to predorsal length.

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[11] The palatine teeth in larger specimens of *A. filamentosus* from Madeira are in a broad band while those on a fish of intermediate size from the Azores are intermediate between a band and two parallel rows. These rows probably fuse, with growth, to form a band.

[12] The anterior rays, which are filamentous in male *A. filamentosus* but not greatly produced in *A. cadenati*, may be broken in this specimen.

Color. In alcohol, the head purple, the body yellowish with purple blotches of irregular size and not bilaterally symmetrical. Pectoral and anal fins colorless; ventral fins, especially the thickened tips of the outer rays, reddish; the tips of anterior four dorsal rays black, the rest of the fin dusky; the caudal fin dusky with a darker spot on the middle of each lobe.

Mr. Harvey R. Bullis, Jr. has generously provided a description of the fresh color of three specimens, caught north of western Cuba,[13] as follows: The belly forward of the vent is silvery; behind the vent it is flesh-colored. The sides of the body are strongly opalescent and iridescent but interrupted by a series of transverse bands. The first strong band starts at the origin of the dorsal fin and extends to the middle of the base of the dorsal. The second starts just posterior to the base of the dorsal and extends horizontally about halfway to the adipose fin. There is another band just before the caudal fin. The dorsal, pectoral and pelvic fins are traversed by bands of yellow and white, interspersed with a few light-blue iridescent areas. The anal fin is transparent save for a few faint yellow bands. The caudal fin is horizontally barred with yellow and white and, except in one of the three specimens, brown. The upper jaw is yellowish; the lower colorless. The cheeks are strongly iridescent, the background color being blue-green. The space between the eyes is dark green, and the snout is a light yellow and white. The iris of the eye is a reddish gold, with a trace of a greenish cast; the pupil is black. The lining of the opercular flaps is an iridescent yellow. The adipose fin is transparent save for some yellow at the tip. In the smallest specimen, the ends of the first few dorsal rays are marked with black, against a greenish sheen, and the outer ends of the largest pelvic rays are barred with orange. In this specimen the olive-yellow markings on the body are mostly confined to the area above the lateral line, and there is a series of small black markings along the lateral line.

Synonyms and References:

Aulopus filamentosus (*non* Cloquet), Springer and Bullis, Spec. Sci. Rep. Fish., U.S. Fish Wildl. Serv., 196, 1956: 53 (listed, based on specimen later designated type of *A.nanae*); Briggs, Bull. Florida St. Mus., *2* (8), 1958: 257 (listed, from Springer and Bullis, 1956).

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Family Bathypteroidae

GILES W. MEAD
Museum of Comparative Zoology
Harvard University

Reprinted from Memoir Sears Foundation for Marine Research, I (5), 1966: 114–146.

Family Bathypteroidae[1]

GILES W. MEAD[2]
Museum of Comparative Zoology
Harvard University

Characters. MODERATELY SLENDER DEEP-WATER BOTTOM FISHES, 4–18 INCHES LONG, WITH SOME VERY ELONGATED FIN RAYS; THE OUTER VENTRAL RAYS, THE UPPERMOST AND LOWERMOST PECTORAL RAYS, AND THE LOWER CAUDAL RAYS, OR A COMBINATION OF THESE PROLONGED IN ONE OR ANOTHER OF THE SPECIES. Body compressed posteriorly, almost circular in cross section anteriorly. Snout depressed and flattened above. Eye minute, laterally directed, horizontally elliptical, and located immediately above the series of lateral-line pores adjacent to the upper jaw bones. Interorbital space broad and slightly concave; circumorbital bones small and poorly ossified, the supraorbital fused with the skull.

Scales present on cheeks and body; the scales cycloid, usually with smooth free edge but strongly pectinate in a few; scales on cheeks about the same size as those on body; scales also present on base of caudal fin and, in perfect specimens, on the gular fold. Lateral line uninterrupted and continuing onto the base of the caudal fin above the midcaudal ray.

Dorsal fin in anterior half of body but more posteriorly placed than in the Aulopidae or Chlorophthalmidae, its origin well behind a vertical at insertion of ventral fin; the rear end of its base over, or only slightly anterior to, origin of anal fin; rays 11–15. Anal fin in posterior half of body but farther forward than in related groups; its base shorter than that of dorsal fin, the fin composed of 8–13 rays. Bases of dorsal and anal fins shorter than head. Caudal fin forked, the lower lobe, exclusive of the 2 lower simple principal rays, usually longer than the upper; principal rays 19 (I-16-II), the 2 lower rays stiffened and prolonged, and occasionally fused; these 2 rays, and frequently one or both of the branches of the ray immediately above the simple rays, formed of

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[1] Including the family Benthosauridae of Goode and Bean (*17*); see *Benthosaurus*, p. 117.

[2] Most of this study was done while the author was with the Ichthyological Laboratory, U.S. Fish and Wildlife Service, U.S. National Museum.

segments which are much shorter than those of the upper rays. Ventral fin situated about midway between gill opening and origin of dorsal fin, its origin in central third of body length, the fin composed of 8 or 9 rays, the outer 2 frequently fused and prolonged; the fins, when expanded, lying in an oblique plane. Pectoral fin either undivided and situated high on shoulder (*Benthosaurus*), or in a more lateral position and divided into two parts; with or without prolonged rays. Adipose fin present or absent; when present, located at a variable distance posterior to a vertical at posterior end of base of anal fin.

Position of anus variable. Anal papilla small.

No luminous organs.

Lower jaw terminal. Suspensorium posteriorly inclined. Upper jaw extending beyond eye for a distance of more than half the length of the head; one slender supramaxillary; posterior end of maxillary dilated. Tongue very small or absent, the glossohyal supporting element in a horizontal position when tongue is present; when absent, glossohyal bound in an oblique position to basihyal bones.

Teeth minute but sharp; some slightly barbed; some depressible; none enlarged; present on jaws and usually on vomer and palatines, the teeth on these bones about equal to one another in size; none on tongue.

Gill arches extending far forward into mouth, their anterior attachments near tip of isthmus and far in advance of angle of gape. Gill rakers of moderate length and of the usual lath-like shape. Branchiostegal membranes broad and separate from one another and from the isthmus, overlapping anteriorly, and crossed near the tip of the jaw by a thick but narrow gular fold; the membrane extending posteriorly beyond opercular flap. Interopercle not reduced. Branchiostegal rays 11–13, of which 4 or 5 are inserted on the epihyal. Opercular flap thin and membranous, its posterior edge formed by both the opercle and the subopercle.

Vertebrae 49–60.

All western Atlantic species monoecious.

Fin-ray Modifications. The very long fin rays of the Bathypteroidae are of special interest. In the genus *Benthosaurus*, the elongated outer ventral and lower caudal rays form a tripod on which the fish stands, as has been shown in recent deep-sea photographs.[3] It is not yet known whether the other bathypteroids that have stout and elongated ventral and caudal rays (*Bathypterois viridensis* and its allies) behave similarly. In many of the species of *Bathypterois*, the upper rays of the pectoral fin are fused basally and often extend posteriorly beyond the caudal fin. The structure of the bones and muscles which support these rays (*20*: 185, pl. 48 B) and observations made on the position of these rays in newly caught specimens indicate that in life they are arched forward over the head. They probably are organs of touch. No function is suggested for the strong lower pectoral ray of *Bathypterois quadrifilis*.

Another unique specialization is the thickening and curvature of the posterior ventral procurrent caudal fin rays (see *Bathypterois phenax*, p. 136; *B. quadrifilis*, p. 141). In certain species these rays form a strong and well-developed subcaudal hook, which is present in juveniles (about 60 mm) as well as in adults. Collett (*12*), who suspected that these fishes used the caudal fin for support on the bottom, suggested that this notch enabled the fish to lower the lower lobe of its caudal fin farther than it otherwise might. But it is of interest in this connection that the only species which is positively known to rest on the bottom supported in part by its caudal fin (*Benthosaurus*) does not have the subcaudal notch, nor do the species of *Bathypterois* most closely related to *Benthosaurus* (*Bathypterois viridensis* and its allies). The subcaudal notch may, on the other hand, serve as a device for cleaning certain of the elongate fin rays. The species that have the notch lack outer ventral rays long enough to reach the caudal peduncle, but these species do have stiffened tactile upper pectoral rays which could be drawn through the notch to scrape off foreign matter.

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[3] See p. 121. Murray and Hjort (*26*: 687), however, suggested that species such as *Benthosaurus grallator* are midwater forms and that the elongated fin rays serve as flotation structures.

Relationships. These fishes are most similar to *Ipnops* of the Ipnopidae (p. 147), from which they differ principally in the bizarre form of the fins and in eye structure. *Ipnops* lacks the small but otherwise normally formed lateral eyes of *Bathypterois* and has, instead, broad and flat photoreceptors which lie beneath the frontal bones on top of the head (see p. 150).

Reproduction. Several species at least are monoecious (Mead, *25*). Definite ovotestes have been found in *Benthosaurus grallator*, *Bathypterois* (*Hemipterois*) *viridensis*, *Bathypterois* (*Bathypterois*) *longipes*, *B.* (*B.*) *bigelowi*, and *B.* (*B.*) *quadrifilis*. The ova are extruded through an ovipore located between the anus and the short anal papilla. The male sex products reach the exterior together with the urinary excrement through a urogenital pore in or near the anal papilla. Both male and female gametes in advanced stages of maturation may be found in a single individual, but it is not known whether cross- or self-fertilization occurs. Neither fertilized ova nor larvae have been found.

Range and Habitat. Representatives of the Bathypteroidae are known from deep waters of all tropical and temperate oceans. Although some authors have concluded that they are midwater forms, all known western Atlantic specimens were taken in bottom-trawl or dredge hauls, and almost all the extralimital captures were also made with bottom gear. A 20-mm juvenile, identified only to genus, has been reported from the eastern Atlantic;[4] verification of its identity is needed. The bathypteroids are usually found over soft muddy bottoms.

The shallowest substantiated record of any bathypteroid is the specimen of *Bathypterois bigelowi* which was taken in the western tropical Atlantic at 260 fathoms (p. 133); the deepest that of a series of eastern Atlantic specimens of *B. longipes* caught by the

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[4] Roule and Angel (*32*) reported and described this fish, from PRINCESSE-ALICE St. 815. It was identified as a *Bathypterois* on the basis of fin formula and placement. In a later paper (*33*: 128), these authors provided the locality data: 30°47′ N, 24°52′45″W, surface, July 10, 1897; they noted two species taken at that station, both larval, and recorded then as "*Stomiatella A, St. B*". These were described and figured, but no mention was made of the 20-mm *Bathypterois* from the same station. In length of specimen and fin structure, "*Stomiatella B*" agrees with the earlier description of the juvenile *Bathypterois*, and the "*Stomiatella B*" designation may be a reidentification of the same specimen. This fish is probably not a bathypteroid but a stomiatoid isospondyl, as Roule and Angel indicate in their account of *Stomiatella*.

Swedish ALBATROSS at 5600 m. Their abundance on the bottom is not uniform, and certain localities have produced more than their share of these fishes: the western Caribbean series of OREGON stations which produced scores of *B. bigelowi*; the GALATHEA trawl haul in the Gulf of Panama at 915 m which caught 42 specimens;[5] and the series of *B. longipes* caught by the Swedish ALBATROSS (*28*). In the report of this last collection, Nybelin has noted that *B. longipes*, a species that prefers cold bottom water (4.17–4.44° C), was by far the commonest species in the ALBATROSS collections from below 4000 m. The total number caught, however, was only 20.

Genera. The bathypteroid species are here divided between the two genera *Benthosaurus* and *Bathypterois*.

Key to Genera

1a. Pectoral fin not divided into two parts and without greatly prolonged rays, none extending beyond origin of anal fin; outer ventral and lower caudal rays longer than standard length; no adipose fin. *Benthosaurus* Goode and Bean 1886, below.

1b. Pectoral fin divided into two distinctly separate parts, the uppermost pectoral ray prolonged, extending beyond origin of anal fin; outer ventral and lower caudal rays never longer than standard length; adipose fin usually present.[6] *Bathypterois* Günther 1878, p. 122.

Genus *Benthosaurus* Goode and Bean 1886

Benthosaurus Goode and Bean, Bull. Mus. comp. Zool. Harvard, *12* (5), 1886: 168; type species, by monotypy, *Benthosaurus grallator* Goode and Bean 1886; eastern Gulf of Mexico.

Generic Synonym:

Skagerakia Nybelin, Ark. Zool., Uppsala, *38* B (2), 1946: 4; type species, by monotypy, *Skagerakia nilssoni* Nybelin 1946, equals *B. grallator* Goode and Bean 1886; eastern Atlantic.

Characters. Pectoral fin not divided into two parts, inserted high on shoulder, its base strongly oblique, forming about a 45° angle with the horizontal; uppermost rays not greatly stiffened or prolonged, not extending beyond anal fin. Ventral fin with outer rays and caudal fin with lower principal rays tremendously prolonged, longer than standard length. Adipose fin lacking. Anterior end of supramaxillary failing to reach rear edge of eye by a distance about equal to length of supramaxillary. Gill rakers on first arch 33 or fewer.

Species. All known specimens are here referred to *Benthosaurus grallator*. The second nominal species, *B. nilssoni* (Nybelin), was compared by Nybelin (*27*: 32) to Goode and Bean's original and subsequent descriptions of *B. grallator*, but these accounts do not adequately describe the type material. A further comparison of American material with the detailed descriptions of eastern Atlantic specimens provided by Koefoed (*22*: 64) and Nybelin (*27*) has revealed only a few minor morphometric differences.

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[5] Bruun (*11*), species name not given.

[6] Adipose fin present in all known western Atlantic specimens.

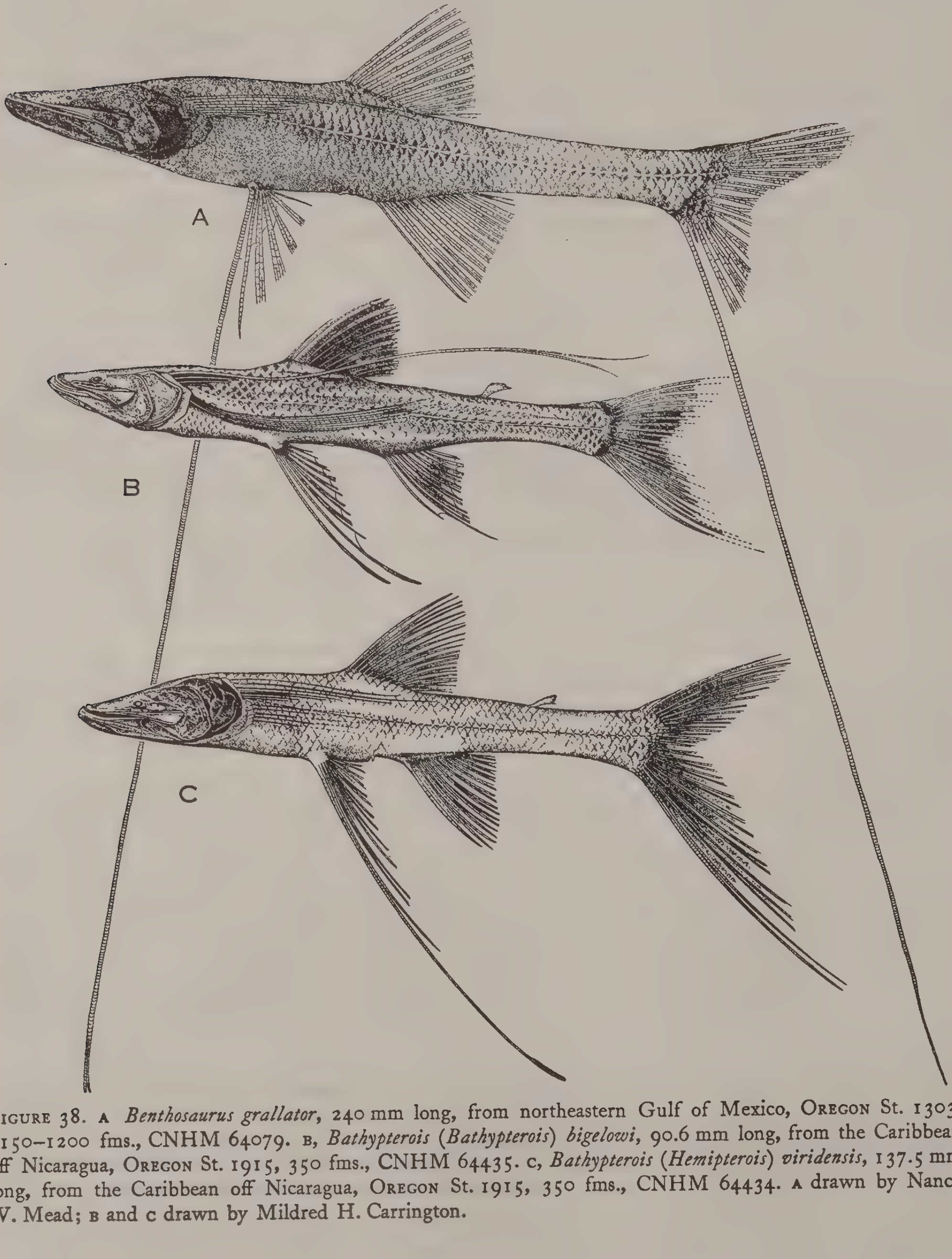

Figure 38. a *Benthosaurus grallator*, 240 mm long, from northeastern Gulf of Mexico, Oregon St. 1303, 1150–1200 fms., CNHM 64079. b, *Bathypterois* (*Bathypterois*) *bigelowi*, 90.6 mm long, from the Caribbean off Nicaragua, Oregon St. 1915, 350 fms., CNHM 64435. c, *Bathypterois* (*Hemipterois*) *viridensis*, 137.5 mm long, from the Caribbean off Nicaragua, Oregon St. 1915, 350 fms., CNHM 64434. a drawn by Nancy W. Mead; b and c drawn by Mildred H. Carrington.

Benthosaurus grallator Goode and Bean 1886

Figure 38 A

Study Material. Five western North Atlantic specimens, 150.0–290.0 mm: one, 258.0 mm SL, ALBATROSS St. 2222, 39°03′15″N, 70°50′45″W, 1537 fms., Sept. 6, 1884, USNM 35651; 1, 240 mm, ALBATROSS St. 2571, 40°09′30″N, 67°09′W, 1356 fms., Sept. 1, 1885, USNM 44675; 3, 150.0–290.0 mm, OREGON St. 1303, 28°47′N, 87°50′W, 1150–1200 fms., May 26, 1955, CNHM 64079, TU 16531.

Distinctive Characters. Those of the genus.

Description. Proportional dimensions in per cent of standard length, based on the type specimens and three additional fish, 150 to 290 mm long, caught in the Gulf of Mexico at OREGON St. 1303.

Body: greatest depth 12.9–15.6; depth at origin of anal fin 12.5–14.1.

Caudal peduncle: least depth 6.0–7.2.

Head: length 26.1–28.7.

Snout: length 7.9–8.6.

Eye: diameter 0.9–1.1

Interorbital: width 7.5–8.8.

Premaxillary: length 18.6–20.3.

Dorsal fin: length of base 12.9–13.6.

Anal fin: length of base 11.7–13.2.

Caudal fin: length of lower ray 127.0–145.0.

Ventral fin: length 135.0–164.0.

Pectoral fin: length of longest ray 27.5–39.6.

Distance from snout to origin of: dorsal fin 46.8–48.6; anal fin 57.1–59.3; ventral fin 37.8–40.1; pectoral fin 24.1–24.8.

Lateral-line scales: 52–54.

Branchiostegal rays: 10 or 11.

Gill rakers: on first arch 8 or 9 + 1 + 19–23 = 28–33.

Fin rays: dorsal 13 (occasionally 12); anal 13; caudal I-16-II (the lower 2 inseparably fused); ventral 8 (the 1st and 2nd fused and indistinguishable from one another in large specimens); pectoral 9 or 10.

Vertebrae: 53 or 54, including urostyle.

BODY compressed, snout depressed, the body deepest at dorsal origin, this depth 1.8–2.1 in hl; its depth at origin of anal fin 2.0–2.1 in hl; its greatest width 1.6–1.8 in greatest depth. Least depth of CAUDAL PEDUNCLE 3.9–4.3 in hl. SCALES present on postorbital part of head, gular fold, isthmus, body and bases of caudal lobes, the scales cycloid and deciduous; almost all missing in all study specimens. LATERAL LINE well developed, beginning above pectoral origin and terminating on upper caudal lobe.

HEAD 3.4–3.8 in SL, nearly flat above and anterior to eye; the lower jaw terminal. SNOUT 3.2–3.4 in head, its tip indented for reception of mandibular symphysis when mouth is closed; snout pierced above by sensory pores and nostrils; a few mucous and sensory pores below and before eye. EYE minute, slightly longer than high and set in a poorly defined elliptical orbit, its horizontal diameter about a third of the greatest width of the maxillary, 7.6–8.8 in length of snout. NOSTRILS well developed, a short flap on the membrane between anterior and posterior nostril; anterior nostrils slightly tubular. Interorbital width 3.3–3.4 in hl. Opercular bones thin but well ossified; subopercle well developed. Gill flap extending well beyond base of pectoral fin. Branchiostegal membranes broad, projecting beyond operculars posteriorly, joined to each other anteriorly under the well-developed gular fold.

Gill rakers well developed on all four arches, which extend far forward into the mouth; the rakers lath-like, flattened and spiny, the longest on 1st arch about twice the length of the opposite gill filament.

Gape large. Mandibles broad and heavy, the outer surface of each with a prominent row of lateral-line pores. Symphysial knob well developed and toothless, received by an indentation at tip of snout when mouth is closed. Premaxillary long, 1.4 in hl. Maxillary broad, its posterior third surmounted by an elongate supramaxillary, its front end separated from the eye by a distance equal to the length of the supramaxillary.

Teeth present on jaw and vomer; palatines, tongue, and tips of both jaws toothless. Mandibular teeth in a broad band; the teeth round in cross section basally, recurved, depressible, and barbed at their tips. Premaxillary teeth similar to mandibular teeth but somewhat larger and more numerous. Some lateral jaw teeth directed outward. Vomer with a large and well-developed patch of depressible teeth on each vomerine knob, and, in the smaller fish (150 mm) only, a single transverse row of teeth between these patches (as in some species of *Chlorophthalmus*); vomerine teeth similar to those on jaws.

Dorsal fin inserted on a vertical midway between insertion of ventral fin and origin of anal, the first ray simple, the rest branched. Predorsal distance 2.1 in SL; the length of base 2.0–2.1 in hl. Anal origin under, or slightly before, rear end of base of dorsal; first ray simple, the rest branched. Preanal distance 1.7–1.8 in SL; the length of base 2.1–2.4 in hl. Caudal fin highly modified, the base of the principal rays not vertical but forming an oblique line sloping downward and forward. The uppermost principal ray simple; the lower 2 rays simple, fused, and almost indistinguishable from each other, stiffened and greatly prolonged. Caudal lobes, exclusive of the simple rays, asymmetrical, the upper lobe longer. Base of lower extended caudal rays supported by closely-applied and buried ventral procurrent caudal rays (from X-ray photographs). Ventral fin has the outer 2 rays similar in length and strength to the lower caudal rays, inseparably fused throughout, stiffened, and identifiable as separate elements only in the young specimen; preventral distance 2.5 or 2.6 in SL. Pectoral fin inserted high on shoulder, entire, its base sloping downward and backward at about a 45° angle; all rays simple, the most dorsal ray the longest. Prepectoral distance 4.0–4.2 in SL.

Color. In alcohol, dark brown or black, the body mottled, since the edge of each scale pocket at which the scale was inserted is colorless. Bases of all fins dusky; the fins colorless. Head, especially the opercles and branchiostegal membranes, black. Linings of mouth, pharyngeal and abdominal cavities black.

Fresh specimens similar except for the pinkish color at the tips of the anterior 4 dorsal, all caudal, and anterior 6 anal rays. Interradial membranes of ventral fins reddish. Pupil of eye an iridescent gold.

Remarks. Nothing is known of the development or life history of this bizarre species. The function of the greatly prolonged ventral and caudal fin rays has been determined by the use of recent developments in deep-sea photography, for two underwater photographs show this species resting on the ocean floor on the tips of the outer ventral and lower caudal rays,[7] and it is said to hop along the bottom like a cricket.

Range. B. grallator is now known from six western Atlantic localities: four in the Gulf of Mexico,[8] and two off the Atlantic states. The depths of capture: 2104–3384 m.

This species has been taken twice in the eastern Atlantic, once by the Michael Sars and later by the Swedish "Skagerak" Expedition, at 2865 and at 2150–2300 m respectively;[9] and deep-sea photographs of fishes that are probably of this species have been taken in the Mediterranean at depths of 2347 and 2132 m.[7] The only non-Atlantic capture was by the Danish Galathea Expedition, in a trawl haul in the Mozambique Channel at a depth of 3400 m.[10]

Synonyms and References:

Benthosaurus grallator Goode and Bean, Bull. Mus. comp. Zool. Harvard, *12* (5), 1886: 168 (orig. descr. 24°33′N, 84°23′W, 1850 fms.); Agassiz, Bull. Mus. comp. Zool. Harvard, *15* ("Three Cruises of the Blake"), 2, 1888: 32, fig. 218 (orig. fig.; no descr. or loc.); Goode and Bean, Smithson. Contrib. Knowl., *30*, 1895: 62, pl. 19, fig. 73 (descr.; w. N. Atl.); Jordan and Evermann, Bull. U.S. nat. Mus., *47* (1), 1896: 543 (from Goode and Bean, 1895); Jordan and Evermann, Rep. U.S. Comm. Fish (1895), App. 5, 1896: 297 (listed); Garman, Mem. Mus. comp. Zool. Harvard, *24*, 1899: 400 (range); Murray and Hjort, Depths of Ocean, 1912: 688, fig. 502, and elsewhere (descr., eyes *cf.* those of rel. species); Koefoed, Rep. 'Michael Sars' N. Atlantic Deep Sea Exped., *4* (1), 1927: 64 (descr. Michael Sars spec., St. 53, 34°59′N, 33°01′W, 2865 m); Parr, Bull. Bingham oceanogr. Coll., *3* (3), 1928: 23 (in key, diagn.); Jordan, Evermann and Clark, Rep. U. S. Comm. Fish. (1928), App. 10, 1930: 166 (listed); Fowler, Bull. Amer. Mus. nat. Hist. *70* (1), 1936: 361, fig. 172 (descr. from Goode and Bean, 1895); Grey, Fieldiana: Zool., *36* (2), 1956: 131 (complete distr. data and refs.); Briggs, Bull. Fla. St. Mus., Biol. Sci., *2* (8), 1958: 258 (listed, from Goode and Bean, 1895); Grey, Fieldiana: Zool., *39* (16), 1958: 159 (from Oregon St. 1303; descr., *cf. Skagerakia nilssoni*).

Skagerakia nilssoni Nybelin, Ark. Zool., *38 B* (2), 1947: 4, fig. 3–4 (orig. descr., photo.; E. Atl., Swedish "Skagerak" 35°43′N, 8°16′W, 2150–2300 m); Nybelin, Göteborgs VetenskSamh. Handl., (B) *5* (16), 1948: 32, pl. 2, fig. 3, pl. 3, fig. 3 (descr. Swedish "Skagerak" spec., *cf.* Michael Sars and American Albatross and Blake coll.).

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7. References to these remarkable photographs are given in *Synonyms and References* under *Benthosaurus* sp. Since all specimens actually collected in the Atlantic can be referred to *B. grallator*, these photographs are probably of this species. Among the other known bathypteroid species, only *Bathypterois* (*Hemipterois*) *viridensis* has ventral and caudal rays of similar length and strength, but these rays, in all known specimens, are somewhat shorter than those shown in the photographs; and the species is found in water shallower than the depths at which the photographs were taken.
8. Oregon St. 1303, see *Study Material* above; Blake St. clxxiv, probably 24°33′N, 84°23′W, 1850 fms.; Oregon St. 2575, 27°06′N, 89°13′W, 1200–1100 fms., 40-ft. trawl, July 29, 1959; Oregon St. 2577, 27°48′N, 88°45′W, 850–1100 fms., 40-ft. trawl, July 30, 1959; and Oregon St. 2820, 28°23′N, 88°21.5′W, 1000 fms., July 15, 1960. Atlantic coast records: Albatross St. 2222 and 2571, see *Study Material* for data. Grey (*18*: 320) has pointed out that the data for Blake St. clxxiv given by Goode and Bean do not agree with those given by Sanderson Smith (*34*), who has given a depth of 1920 fms. and a locality off Guadeloupe Island for this station. I have been unable to locate the original Blake log book. The several labels now in the jar with this specimen (MCZ 27924) give the Gulf of Mexico locality.
9. Both of these records have been published; see Koefoed (*22*) and Nybelin (*27*).
10. Reported as "*Benthosaurus*" by Bruun (*11*). This fish should be critically compared with Atlantic specimens.

Benthosaurus nilssoni, Dollfus, Trav. Inst. scien. Chérifien, (zool.) 6, 1955: 39 (listed).

Benthosaurus sp. Le Danois, Millot, Monod, and Budker, Fishes of the World, 1957: 175, fig. (photo. of living spec. on sea floor; no loc. data; also in an earlier French edition, not seen). MacLeish, Life, *37* (13), 1954: 100 (fig. from "bathyscaphe", Medit. near 7700 ft.); Edgerton, Nat. geogr. Mag., *107* (4), 1955: 526, 536, fig. (Medit., 7000 ft. reported to spring across the bottom like a cricket); Houot and Willm, Two Thousand Fathoms Down, 1955: pl. opposite p. 129 (photo. spec. resting on "tripod" on bottom, no loc. or depth).

Benthosaurus amblyops Bernard, Ann. Inst. océanogr. Monaco, *35*, 1958: 323, pl. 23 (new name based on Medit. bathyscaphe photo; possibly not a *Benthosaurus* but a *Bathypterois*).

Negative Reference:

Benthosaurus grallator, Springer and Bullis, U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish., *196*, 1956: 55 (Oregon St. 1019; equals *Bathypterois* (*Hemipterois*) *viridensis* (Roule); spec. re-examined, USNM).

Genus *Bathypterois* Günther 1878

Bathypterois Günther, Ann. Mag. nat. Hist., (5) *2*, 1878: 183; type species, designated by Jordan and Evermann, Bull. U.S. nat. Mus., *47* (1), 1896: 544, *Bathypterois longifilis* Günther.[11]

Characters. Pectoral fin formed of two separate parts, the upper consisting of 2–5 rays. In one group of species (subgenus *Bathypterois*), the upper 2 pectoral rays are prolonged, those immediately below them short, and the upper part is separated from the lower by a wide interspace. In the second group (*Hemipterois*), all rays of the upper part are well developed, and the space between the upper and lower parts is only a little greater than that between the rays in adjacent parts of the fin in juveniles but becoming wider with growth. Lower caudal fin rays never longer than the fish, although frequently prolonged. Lower caudal rays, outer ventral rays, and lower pectoral ray variously prolonged or normal. Adipose fin usually present. Gill rakers on first arch 33 or more.

Remarks. The several species of *Bathypterois* are widely distributed throughout the major oceans. Although certain species, for example *B. longipes*, are now thought to be among the more common of the deep-sea bottom fishes, nothing is known of the life-history or biology of any.

Key to Subgenera and North Atlantic Species

1a. Uppermost pectoral ray not notably thicker at its base than its neighbor; all rays of upper part of pectoral fin well developed; fewer than 6 rays in lower part of pectoral fin. Subgenus *B.* (*Hemipterois*).
viridensis Roule 1916, p. 124.

1b. Uppermost pectoral ray at least twice as thick at its base as that of its neighbor; lower rays of upper part of pectoral fin poorly developed; more than 6 rays in lower part of pectoral fin. Subgenus *B.* (*Bathypterois*).

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[11] Generic synonyms have been allocated to the subgenera, see pp. 123 and 129. The generic name was misspelled *Brachypterois* by Jordan and Seale (*21*) and *Bathypoterrois* by Bertin (*8*).

2a. Scales behind base of lower part of pectoral fin strongly pectinate; lowermost ray of lower part of pectoral fin long and conspicuously thicker than its neighbor. *quadrifilis* Günther 1878, p. 141.

2b. Scales behind base of lower part of pectoral fin not pectinate; lowermost ray of lower part of pectoral fin not longer or thicker than its neighbor.

  3a. Subcaudal notch present.

    4a. Eight ventral rays; anal origin behind end of base of dorsal fin. *dubius* Vaillant 1888.
    Eastern Atlantic.

    4b. Nine ventral rays; anal origin under end of base of dorsal fin. *phenax* Parr 1928, p. 136.

  3b. Subcaudal notch absent.

    5a. Lower rays of upper part of pectoral rudimentary and not connected by a black membrane; interradial membrane of dorsal fin colorless; body uniformly dark; caudal lobes dusky but without conspicuous black spots at their bases; membrane between central caudal rays colorless. *longipes* Günther 1878, p. 133.

    5b. Lower rays of upper part of pectoral fin connected by black membrane; interradial membrane of dorsal fin black; body darker above than below; prominent black spots at bases of upper and lower caudal lobes: membrane between central caudal rays black. *bigelowi* Mead 1959, p. 130.

Subgenus *Hemipterois* Regan 1911

Hemipterois Regan, Ann. Mag. nat. Hist., (8) 7, 1911: 127; type species, by original designation, *Bathypterois guentheri* Alcock, Ann. Mag. nat. Hist., (6) 4, 1889: 450; Indian Ocean.

Subgeneric Synonym:

Belonepterois[12] Roule, Bull. Inst. océanogr. Monaco, 320, 1916: 13; type species, by original designation, *B. viridensis* Roule 1916; eastern Atlantic off the Cape Verde Islands, 1477 m.

Subgeneric Characters. Space between the upper and lower parts of pectoral fin far less marked in *B.* (*Hemipterois*) than in *B.* (*Bathypterois*), the space scarcely greater than that between the neighboring rays of either part in juveniles but increasing with growth, the two parts of the fin well separated in adults. The two uppermost rays of the upper part separate from one another, well developed, stiffened, and prolonged; the lower rays of the upper part well developed also, the longer of these at least a quarter of the length of the two prolonged upper rays (these rays in *B.* [*Bathypterois*], though occasionally well developed, are small compared with the two prolonged rays; *e.g. B. bigelowi*, Fig. 38 B). Base of caudal fin heavily scaled. Subcaudal notch lacking. Ventral fin with 2nd ray more slender than 3rd.

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[12] Occasionally misspelled *Belonopterois*.

Size. These fishes reach a length of about ten inches, exclusive of the prolonged fin rays.

Range. The species are now known from moderately deep waters (350–1100 fathoms) of the eastern and western tropical and north temperate Atlantic, off Japan, and in the Indian Ocean.

Species. There are two known species: *B.* (*H.*) *guentheri* Alcock and *B.* (*H.*) *viridensis* Roule.[13] These species cannot be critically compared until more specimens have been caught, for the fin form and placement and the method of counting and reporting rudimentary and fused rays varies greatly. The western Atlantic species is included in the *Key to Subgenera and North Atlantic Species*, p. 122.

Bathypterois (*Hemipterois*) *viridensis* (Roule) 1916

Figure 38c

Study Material. Twelve specimens, 65.1–197.0 mm: one, 197.0 mm, Harvard-Havana Exped., ATLANTIS St. 2990B, 23°16′30″N, 80°12′W, 415 fms., March 14, 1938, MCZ 39389; 1, 65.1 mm, Harvard-Havana Exped., ATLANTIS St. 3469, 23°12′N, 81°22′W, 425 fms., May 9, 1938, MCZ 35589; 1, 160.0 mm, CAPT. BILL St. 115, 44°42′N, 66°43′W, 490–540 fms., July 29, 1952, MCZ 37642; 1, 80.0 mm, OREGON St. 1019, 24°16′N, 83°22′W, 375 fms., April 16, 1954; 1, 111.0 mm, OREGON St. 1906, 12°19′N, 82°27′W, 325 fms., Sept. 11, 1957, CNHM 64423; 2, 92.5 and 120.5 mm, OREGON St. 1907, 12°25′N, 82°23′W, 400–425 fms., Sept. 11, 1957, CNHM 64425; 1, 179.0 mm, OREGON St. 1914, 13°06′N, 82°13′W, 350 fms., Sept. 12, 1957, CNHM 64433; 1, 135.5 mm, OREGON St. 1915, 13°13′N, 82°13′W, 350 fms., Sept. 12, 1957, CNHM 64434; 2, 76.8 and 145.5 mm, south of Tortugas, Florida (Longley Coll., no precise data), USNM 117215; 1, 66.3 mm, PAWNEE St. 20, 23°54′10″N, 77°09′W, 710–720 fms., Nov. 3, 1927, BOC 2134.

Comparative material includes: the type of *B. nigrescens* Parr, 61.0 mm, ATLANTIS St. 1478, 25°39′N, 77°18′W, 1050–1100 m, Feb. 20–21, 1933, BOC 3203; and one specimen with characteristics intermediate between *B. viridensis* and *B. guentheri*, from Japan:[14] ALBATROSS St. 4972, 33°25′45″N, 135°33′E, 440 fms., Aug. 30, 1906, USNM 159591.

Distinctive Characters. Body compressed, the snout depressed. Seven well-developed rays in upper part of pectoral fin, surmounted by two small rudimentary rays which are closely applied to the uppermost strong pectoral ray, and much more apparent in juveniles than in adults. Five rays in lower part of pectoral fin. Dorsal fin inserted under, or slightly in advance of, base of last dorsal ray. Background color of body pale; body covered by minute chromatophores which give it a speckled appearance. Adults with two broad conspicuous vertical dark bands, one immediately behind the dorsal fin, another through the posterior part of the caudal peduncle and the caudal fin.

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[13] *B.* (*H.*) *nigrescens* is here tentatively considered a synonym of *B.* (*H.*) *viridensis* Roule; see p. 127.

[14] This appears to be the first Japanese record of the species.

Description. Proportional dimensions in per cent of standard length, based on the 12 specimens referred to above under *Study Material*, 65.1–197.0 mm SL. These specimens, from widely separated western Atlantic localities, illustrate the extreme variability within this species.

Body: greatest depth 12.8–17.3; depth at origin of anal fin 12.0–15.0; greatest width 6.7–9.5.

Caudal peduncle: least depth 7.5–10.1.

Head: length 24.7–29.1.

Snout: length 8.1–9.8 (shorter in specimens from off New England).

Eye: horizontal diameter 1.4–2.4.

Interorbital: width 7.8–9.8.

Premaxillary: length 16.1–18.8 (longer in Caribbean specimens).

Dorsal fin: length of base 11.8–14.8.

Anal fin: length of base 9.0–12.4.

Distance from snout to origin of: dorsal fin 44.2–50.6; anal fin 51.8–58.4; ventral fin 39.4–43.7; upper part of pectoral fin 22.3–25.0.

Distance from: base of last dorsal ray to insertion of adipose fin 20.9–24.8; base of last anal ray to adipose origin 17.6–20.7; insertion of ventral fin to origin of anal fin 14.6–17.7; anus to insertion of ventral fin 8.2–10.1; anus to origin of anal fin 4.9–7.4.

Lateral-line scales: 52–55.

Branchiostegal rays: 12 or 13.

Gill rakers: on first arch 11–13 + 28–30.

Fin rays: dorsal 12–13; anal 11–12; caudal I-16-II; ventral 8, including a second slender simple ray separate from the first in juveniles but inseparably bound to it in adults; pectoral—upper part 7 + 2 short upper rudiments overgrown and not easily found in adults, and lower part 5.

Vertebrae: 50 or 51, including urostyle.

Body compressed, snout depressed, the body deepest at origin of ventral or dorsal fins, the greatest depth 1.5–2.2 in hl; depth at anal origin 1.6–2.3 in head. Least depth of Caudal peduncle 2.4–3.4 in head. Scales present on cheek, body, gular fold and base of caudal fin, the scales cycloid and deciduous, those on gular fold seldom present; articular bone with scales; a slightly enlarged scale in axil of ventral fin. Lateral line simple, well developed, beginning just above base of uppermost pectoral fin ray and extending onto caudal fin well above the center caudal ray, its scales pierced by a single tube.

Snout broad, rounded anteriorly, terminating in a depression that receives the tip of the lower jaw, its length 2.8–3.3 in head. Eye minute, laterally directed, relatively larger in juveniles than in adults, 3.8–7.0 in length of snout. A horizontal row of sensory pores below eye. Nostrils and pores on head well developed, a short flap on the membrane separating the anterior from the posterior nostril. Interorbital 2.8–3.6 in hl. Branchiostegal membranes broad, covered anteriorly by a small gular fold, and extending posteriorly beyond opercles. Isthmus very narrow. Gill arches extending forward far into the mouth, all four bearing rakers.

Gill Rakers on first arch long, the longest about twice the length of the opposite gill filament, each with spines along the inner edge.

MANDIBLE broad and heavy, pierced by a row of pores (opening into a horizontal lateral-line channel) along its outer surface. Symphysial knob well developed, received by a cleft in tip of upper jaw. PREMAXILLARY long and slender, its length about 1.5 in hl. MAXILLARY broad and flattened, broader than horizontal diameter of eye and surmounted by, but not fused with, a slender supramaxillary, the anterior end of which is well behind the eye.

TEETH. A broad band of small conical teeth on mandible; a similar band on premaxillary. The inner teeth larger, slightly recurved, and depressible. A small patch of small teeth usually present behind head of vomer, and occasionally a few minute teeth along front end of palatine. Symphysis of both jaws and tongue toothless.

DORSAL fin inserted over, or immediately posterior to, base of inner ventral fin rays, the predorsal distance 2.0–2.2 in SL; the 1st ray simple, the rest branched, the last divided to its base; the 2nd–4th rays longest. ADIPOSE fin about midway between end of dorsal base and upper caudal fin rays. ANAL fin inserted under base of last dorsal ray or slightly before this vertical, the first ray simple, the rest branched, the 2nd and 3rd rays longest. The preanal distance 1.7–1.8 in SL. CAUDAL fin with 2 lower principal rays simple and greatly prolonged, their tips usually thickened; these 2 rays separable basally in the young but inseparably united in the adults. VENTRAL fin with outer rays always prolonged but of variable length, the 2 outer rays simple; the 2nd slender, the thickness of its base much less than that of the 1st or 3rd ray, and firmly bound proximally to the 1st, the ray sometimes difficult to locate in large adults; tip of outer ray usually thickened, the ray extending beyond end of midcaudal rays in most specimens but falling short of base of caudal in some (*e.g.*, the fish from off New England). Preventral distance 2.3–2.5 in SL.

PECTORAL fin sharply divided into two well-separated parts in adults but less distinctly so in the juveniles. In the smallest available specimens (66.3 and 76.8 mm), the space at the base between the lowermost ray of the upper part and the uppermost ray of the lower part is not more than twice the space that separates neighboring rays in either upper or lower parts. Seven well-developed principal rays in upper part surmounted by 2 additional small "procurrent" rays above which are closely applied to the uppermost strong ray and distinguishable without dissection only in the juveniles. Upper 2 principal rays simple, stiff and curved upward, but separate from each other, and reaching but little farther back than the end of the dorsal base. Five rays in lower part of pectoral fin, all well developed but shorter than those in upper part. Prepectoral distance 4.1–4.5 in SL.

Color. In preservative, body pale; adults with dark broad vertical bands, one behind the dorsal fin, another through the caudal fin and adjacent parts of the caudal peduncle. Pigmentation along edges of scale pockets gives the body a speckled appearance. Head dark. Branchiostegal membranes, lining of mouth, pharyngeal and abdominal cavities black. Caudal and lower part of pectoral fin largely black; the swollen tips of the elongate ventral and caudal rays dark; dorsal, anal, ventral and adipose fins black.

Mr. Harvey R. Bullis, Jr. has provided the following color notes on three specimens caught at Silver Bay St. 1195, between the tip of Florida and western Cuba:

> Coloration of three large specimens shows some variation. The most deeply pigmented specimen is bluish on the head, black under the chin and on the operculum. The pineal window appears as a transverse rectangle. On the body the peritoneal area is bluish. There are three bands over the body which are blackish in color. The first is immediately before the dorsal, second immediately behind it, and the third is in the caudal area confluent with the caudal fin. The dorsal, anal, pelvic and pectoral fins are all transparent. The elongate pelvic rays are tipped with black, the elongate anal ray is white beyond the caudal fin but the tip is also black. The adipose fin is also transparent. The other two specimens are lighter in color, the body bands are much fainter. The upper tip of the caudal of the first specimen is white.

Relationships. The western North Atlantic representatives of *B.* (*H.*) *viridensis* differ in several respects from the type specimen described by Roule (*31*: 35, pl. 1, fig. 3), which was caught off the Cape Verde Islands at a depth of 1477 m. Roule's type differs in fin placement and in certain counts (dorsal—11; anal—9; pectoral—6 + 5; lateral line scales—48). Were it not for the morphometric variability apparent within our western Atlantic series, the eastern and western Atlantic specimens might be considered distinct. If the variability found in the length of produced pectoral, ventral and caudal rays is not genetic, *B.* (*H.*) *viridensis* may be a subspecies of the Indian Ocean *B.* (*H.*) *guentheri* Alcock.[15] Far more material than is now available will be needed before problems such as these can be studied.

Variation. A few comments on the identity of *Bathypterois* (*Hemipterois*) *nigrescens* Parr, a form here included in the synonymy of *B.* (*H.*) *viridensis*, are in order. *B.* (*H.*) *nigrescens* was described from a 61.0-mm specimen collected by the Atlantis off the Bahamas;[16] this specimen differs slightly from the series of western Atlantic *B.* (*H.*) *viridensis* in many body proportions and, according to Parr, who took color notes from the fresh specimen, it is uniformly black (*30*: 19). The species has not been captured since, although the type locality is within the bathymetric and geographic range of *B.* (*H.*) *viridensis*.

A comparison of the body proportions of *B.* (*H.*) *nigrescens* and *viridensis* suggests that the former may be a specimen of the latter with an abnormally shortened caudal section in its vertebral column. Such an abnormality would account for its greater relative depth, its relatively longer predorsal and preanal lengths, and its shorter tail proportions. Unfortunately, the vertebral characteristics of *B.* (*H.*) *nigrescens* cannot be determined, preservation for 25 years in formalin having decalcified the bones to such an extent that the best of several X-ray attempts shows only a few of the heavier thoracic vertebrae and none of the caudals.[17] Counts, and measurements in per cent of standard length, taken from the type of *B.* (*H.*) *viridensis*, follow.

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[15] Alcock (*1*; *2*; *4*, pl. 1, fig. 6; *7*: 157). *B.* (*H.*) *guentheri* was described from specimens taken in the Andaman Sea, 490 fms.; the Bay of Bengal off Andaman Island, 561 fms.; and the Arabian Sea off the Laccadives and Maldives, 636 and 719 fms.

[16] Atlantis St. 1478, 25°39′ N, 77°18′W, 1050–1100 fms., Feb. 20–21, 1933, BOC 3203.

[17] The full vertebral columns of smaller specimens preserved in alcohol following fixation in formalin show clearly in similar X-ray negatives.

Body: greatest depth 17.5; depth at origin of anal fin 16.4.

Caudal peduncle: least depth 9.0.

Head: length 27.5.

Snout: length 9.1.

Eye: diameter 2.2.

Interorbital: width 8.0.

Premaxillary: length 17.0.

Dorsal fin: length of base 13.6.

Anal fin: length of base 10.0.

Longest fin-ray lengths: caudal 59.0; ventral 69.7; pectoral (upper part) 23.0, after Parr (*30*: 19), the specimen having been damaged since his examination of it.

Distance from snout to origin of: dorsal fin 51.0; anal fin 60.6; ventral fin 43.4; pectoral fin 25.3.

Distance from: base of last dorsal ray to adipose fin 20.8; adipose fin to dorsal procurrent caudal ray 13.9.

Gill rakers: on first arch 12 + 1 + 29.

Fin rays: dorsal 12; caudal 1-16-11; anal 11; ventral 8; pectoral—upper part 9 or 10, including the one or two rudimentary rays above the first strong ray, and the lower part 5 or 6.

Since this species is of questionable validity, no further description is presented here.

Range. Most of the known western North Atlantic specimens are listed above under *Study Material*.[18] In the western Atlantic, the known bathymetric range is 350 to 720 fathoms, and the species has been taken from off New England and the Bahamas, in the Straits of Florida and adjacent areas, and in the western Caribbean.

Synonyms and References:

Belonepterois viridensis Roule, Bull. Inst. océanogr. Monaco, 320, 1916: 13 (orig. descr.; St. 1209; off Cape Verde Is.; 1477 m); Roule, Résult. Camp. Sci. Monaco, *52*, 1919: 35, pl. 1, fig. 3 (descr., color fig., based on type); Belloc, Bull. Inst. océanogr. Monaco, 958, 1949: 10 (type spec. recorded).

Bathypterois (*Hemipterois*) *viridensis*, Parr, Bull. Bingham oceanogr. Coll., *3* (3), 1928: 25, fig. 2 (in key, descr. of spec. from PAWNEE St. 20, 23°54′N, 77°09′W, 710–720 fms, Nov. 3, 1927); Parr, Bull. Bingham oceanogr. Coll., *4* (6), 1934: 19 (in key to species of *B*. [*Hemipterois*]).

Bathypterois (*Hemipterois*) *nigrescens* Parr, Bull. Bingham oceanogr. Coll., *4* (6), 1934: 19 (orig. descr.; Tongue of the Ocean).

Bathypterois viridensis, Fowler, Bull. Amer. Mus. nat. Hist., *70* (1), 1936: 359, fig. 171 (descr., from Roule); Longley and Hildebrand, Publ. Carnegie Inst. Wash., 535, 1941: 25 (descr. 2 spec. from S. of Tortugas, Florida); Fowler, Monogr. Acad. nat. Sci. Philad., *6*, 1944: 438 (listed; from Parr, 1928 and 1934); Springer and Bullis, Sp. Sci. Rep. Fish., U.S. Fish Wildl. Serv., 196, 1956: 55 (listed, OREGON St. 1425 and 1426; Gulf of Mexico); Briggs, Bull. Florida State Mus., Biol. Sci., *2* (8), 1958: 257 (listed); Grey, Fieldiana: Zool., *39*, 1959: 328 (descr., OREGON St. 1425, 29°04′N, 88°05′W, 914 m, Sept. 24, 1955).

Bathypterois nigrescens Fowler, Monogr. Acad. nat. Sci. Philad., *6*, 1944: 438 (listed, after Parr, 1934).

Benthosaurus grallator (*non* Goode and Bean), Springer and Bullis, Sp. Sci. Rep. Fish., U.S. Fish Wildl. Serv., 196, 1956: 55 (listed, OREGON St. 1019: spec. redet., USNM).

Bathypoterrois sp., Bertin *in* Grassé (ed.), Traité Zool., *13* (3), 1958: 1903, fig. 1345 (from Roule, 1919; no trivial name given; general account of specializations and biology, from lit.).

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[18] The others, which were not available when this account was prepared, were taken by the SILVER BAY at the following localities: St. 1195, 24°26′N, 83°33′W, 350 fms., June 8, 1959; St. 1196, 24°11′N, 83°21.5′W, 400 fms., June 8, 1959; and St. 1197, 24°15′N, 83°36′W, 500 fms., June 8–9, 1959.

Subgenus *Bathypterois* Günther 1878

Bathypterois Günther, Ann. Mag. nat. Hist., (5) *2*, 1878: 183; type species, designated by Jordan and Evermann, Bull. U.S. nat. Mus., *47* (1), 1896: 544, *B. longifilis* Günther; Pacific off the Kermadec Islands, 520–630 fms.

Subgeneric Synonym:

Synapteretmus Goode and Bean, Smithson. Contrib. Knowl., *30*, 1895: 64; type species, designated by Jordan and Evermann, Bull. U.S. nat. Mus., *47* (1), 1896: 544, *B. quadrifilis* Günther[19]; off Brazil, 770 fms.

Subgeneric Characters. Space between the upper and lower parts of pectoral fin distinct and much more marked in *B.* (*Bathypterois*) than in *B.* (*Hemipterois*), the space much greater than that between the neighboring rays of either part; the two uppermost rays of the upper part fused basally but separate distally, stiffened and prolonged, usually extending to or beyond adipose fin; the lower rays of the upper part always less than a quarter of the length of the elongate upper rays of the upper part. Subcaudal notch present or absent. Ventral fin with 2nd (simple) ray not especially slender basally, frequently fused with the first.

Size. These species reach a length of about 15 inches. Size at maturity is not known.

Range. These are deep-water bottom fishes known from the tropical and temperate oceans of the world. Bathymetric range: 260 to about 3000 fathoms. An excellent resumé of the distribution of the deep-abyssal species has been provided by Grey (*18*: 131–135).

Species. The subgenus *Bathypterois* (*Bathypterois*) includes most of the species in the family. A definition of the 16 named species will not be attempted here, for the phyletic significance of the differences in fin structure, placement and form cannot be determined until many more collections are available for study. A cursory study of the specimens at hand suggests, however, that several additional bathypteroid species remain to be described. The nominal species are *B. ater* Gilchrist (*15*), *B. filiferus* Gilchrist (*15*) and *B. capensis* Gilchrist and von Bonde (*16*: 8), South Africa; *B. dubius* Vaillant (*35*: 124),[20] eastern Atlantic; *B. pectinatus* Mead (*24*), *B. ventralis* Garman (*13*: 256, pl. 55, fig. 1) and *B. pectoralis* Garman (*13*: 257, pl. K, fig. 1), eastern Pacific; *B. antennatus* Gilbert (*14*: 590), *B. atricolor* Alcock (*5*; *7*: 159; *4*, pl. 17), *B. atricolor indicus* Brauer (*10*: 144, pl. 11, fig. 1), *B. longifilis* Günther (*19*: 183; *20*: 185, pl. 47, fig. B, pl. 48, fig. B), *B. longicauda* Günther (*19*: 184; *20*: 188, pl. 26, fig. B),[21] and *B. insularum* Alcock (*3*: 356; *7*: 158; *4*, pl. 32, fig. 1), Indo-Pacific; and the four western Atlantic species considered on the pages that follow: *B. longipes* Günther, *B. quadrifilis* Günther, *B. phenax* Parr, and *B. bigelowi* Mead.

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[19] The strongly pectinate scales beneath the lower pectoral fin, the strong and elongate lowermost pectoral fin ray, and the unusually high vertebral count distinguish the type of *Synapteretmus* (*B. quadrifilis*) from all other Atlantic species and might be considered of subgeneric importance. The Pacific *B. pectinatus*, however, lacks the strong lower ray but has the pectinate scales; it is thus intermediate between *B.* (*B.*) *quadrifilis* and the remaining species here referred to *B.* (*Bathypterois*). *Synapteretmus* cannot be retained.

[20] *B. dubius* is undoubtedly polytypic.

[21] *B. longicauda* may be an aberrant specimen of *B. longipes* Günther.

Bathypterois (*Bathypterois*) *bigelowi* Mead 1959

Figure 38 B

Study Material.[22] The type and 63 additional specimens, 45.0–137.6 mm SL, from the Gulf of Mexico and Caribbean, in CNHM, USNM, and UMML.

Distinctive Characters. Body pale in color (probably greenish in life), darker dorsally than ventrally. Most of dorsal fin membrane black. Membrane between central caudal rays black. A prominent black spot at base of upper and lower caudal lobes. Membrane connecting lower rays of upper pectoral fin black. Proximal half of anal fin membrane black.

Upper pectoral, outer ventral and lower caudal rays prolonged, the tips of the produced ventral and caudal rays typically thickened. Upper prolonged pectoral rays split at a point behind origin of adipose fin. Eight ventral fin rays. Second and third anal rays considerably longer than first or fourth. Usually three rays in upper pectoral fin below the uppermost two fused and prolonged rays. Frequently four lower rays in upper pectoral fin in juveniles; occasionally two in adults, these lower rays well developed and connected by a black fin membrane. Usually 9 (8 to 10) rays in lower part of the pectoral fin, none notably stronger than the others. Dorsal fin situated over or behind a vertical from axil of ventral fin; anal origin well behind end of base of dorsal fin.

Lateral-line scales 48 to 55, the lateral line continuing onto the caudal fin above central caudal ray. Scales behind lower part of pectoral fin base not pectinate. Total number of gill rakers on first arch 40 or fewer. Eye minute, its greatest measure much less than the width of the posterior end of the maxillary.

No notch below caudal peduncle (*cf. B. phenax*, the notch formed by the posterior ventral procurrent caudal rays). Vertebrae 49 to 52.

Description. Proportional dimensions in per cent of standard length, based on 11 specimens, 90.6–131.0 mm, from various localities in the western Caribbean; fin-ray counts included for all available specimens.

Body: greatest depth 12.9–15.8; depth at origin of anal fin 12.1–14.4; greatest width 6.7–8.9.

Caudal peduncle: least depth 7.7–9.0.

Head: length 20.9–24.1.

Snout: length 7.6–8.6.

Eye: horizontal diameter 1.3–1.7.

Interorbital: width 7.3–8.6.

Premaxillary: length 13.4–15.6.

Dorsal fin: length of base 11.5–13.2.

Anal fin: length of base 6.4–8.3.

Caudal fin: length of produced ray 22.7–27.7.

Ventral fin: longest ray 29.1–37.2.

Pectoral fin: longest ray 78.1–98.3.

Distance from snout to origin of: dorsal fin 40.0–45.0; anal fin 57.6–62.0; ventral fin 37.3–42.1; pectoral fin 17.8–21.8.

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[22] The locality, depth and present catalog numbers of most known specimens are recorded in the type description: Mead (*24*). The species has also been taken north of Cuba at all SILVER BAY stations listed in footnote 18, p. 128, and in the Gulf of Mexico at OREGON St. 2824, 29°07′05″N, 88°04′W, 365–395 fms.

Distance from: base of last dorsal ray to adipose fin 21.6–23.9; from base of last anal ray to ventral procurrent caudal ray 30.0–34.7.

Lateral-line scales: 48–55.

Branchiostegal rays: 11 (infrequently 10 or 12).

Gill rakers: 10–12 + 1 + 22–28 = 33–40.

Fin rays: dorsal 11–13 (13 in 35 specimens, 12 in 17, 11 in 1); anal 8–10 (8 in 3, 9 in 44, 10 in 6); caudal i-16-ii (invariable); ventral 8 (invariable); pectoral—upper part 4–6, including the 2 upper fused rays and 2–4 below them (2 in 9, 3 in 92, 4 in 5, both fins of each specimen counted when possible) and lower part 8–10 (8 in 5, 9 in 74, 10 in 22).

Vertebrae: 49–52 in 14 specimens, from OREGON St. 1915, western Caribbean (51 in 8 specimens).

BODY compressed, snout depressed, the body deepest at origin of dorsal fin, 1.5–1.8 in hl, its depth at origin of anal fin 1.6–2.0 in head. Least depth of CAUDAL PEDUNCLE 2.5–3.1 in head. SCALES present on cheeks and body; all scales cycloid, those beneath lower part of pectoral fin not pectinate; base of caudal fin with scales; all other fins naked. LATERAL LINE complete, originating at upper point of gill opening and terminating on caudal fin above central caudal rays.

HEAD 4.1–4.9 in SL, nearly flat dorsally, rounded anteriorly but with a slight indentation at tip to receive the small toothless symphysial knob of lower jaw. SNOUT depressed, its length 2.8–3.3 in head. EYE minute, horizontally elliptical and laterally directed, much smaller than greatest width of posterior end of maxillary, 3.8–6.0 in length of snout; eye relatively larger in juveniles. A horizontal row of about four pores below eye; top of head pierced by nostrils and a pair of longitudinal series of pores. Olfactory organ well developed. NOSTRILS separated by a membrane bearing a short flap. INTERORBITAL 2.7–3.0 in hl. OPERCULAR BONES well developed and firm. BRANCHIOSTEGAL MEMBRANES broad and free from isthmus, extending beyond rear edge of operculum but not reaching insertion of lower part of pectoral fin. Four BRANCHIOSTEGAL RAYS on epihyal, 7 on ceratohyal.

GILL RAKERS present on all four arches, spinulose, flattened; those near angle of first arch about twice the length of the opposing gill filaments.

PREMAXILLARY 1.6–1.8 in head, surmounted by a thin long supramaxillary which terminates anteriorly under rear edge of eye; a small toothless symphysial knob present.

TEETH. A band of minute teeth on premaxillary and mandible, both bands broader anteriorly. A small patch of minute teeth frequently, but not always, present on vomer, and an occasional row of very small teeth on palatine. Tongue toothless. Well-developed patches of pharyngeal teeth.

DORSAL fin inserted well behind bases of inner ventral rays; the predorsal distance 2.2–2.5 in SL; first 2 rays simple, the rest branched. ADIPOSE DORSAL well developed and broad, placed about equidistant between end of dorsal base and base of upper procurrent caudal rays. ANAL inserted well behind a vertical from last dorsal ray; preanal distance 1.6–1.7 in SL; the 1st, and occasionally the 2nd, ray simple, the 2nd or 3rd longest, markedly longer than that in most bathypteroid species. CAUDAL fin with lower 2 principal rays simple and prolonged, their ends frequently slightly thickened; lower branch of the branched ray immediately above the simple rays also prolonged; the segments forming the two simple rays and this lower branch of the first divided ray much shorter than those of the rays above them; these segments become shorter distally. No subcaudal notch (*cf. B. phenax*, p. 136). VENTRAL fin with 2 outer rays simple, produced, typically thickened at the tips, extending beyond base of anal fin in adult; distance between snout and insertion of ventral fin 2.4–2.7 in SL.

PECTORAL FIN with upper 2 rays united basally, separate distally, the split posterior to origin of adipose fin; lower rays of upper part of fin well developed and connected by a black fin membrane; usually 4 such rays in the juvenile but typically 3 in the adult, occasionally 2. Lower part of fin typically with 9 (8–10) rays, well developed and stiffened, none notably stronger than the others, about equal to one another in thickness basally, arching slightly upward, the longer extending beyond end of base of dorsal fin. Prepectoral distance 4.6–5.6 in SL.

Color. In alcohol, background pale, stippled below the midline with small black spots and darkened above with diffuse dark pigmentation in each scale pocket, the margin of which is pigmentless; thus the body is darker dorsally than ventrally; head and ventral surface of body anterior to ventral fin darker. Mouth, branchiostegal membrane, pharyngeal and abdominal cavities black. Lower part of pectoral fin and ventral fins colorless; membranes connecting lower rays of upper part of pectoral fin, dorsal rays, and midcaudal rays black; proximal half of anal fin membrane black. A large conspicuous black spot at base of upper and of lower caudal lobes.

Fresh specimens greenish in general body color.

Relationships. *B. bigelowi* is the most closely related to *B. longfilis* Günther, a species that the CHALLENGER trawled at 520 and 630 fathoms off the Kermadec Islands in the South Pacific but has not since been reported. Each one of the specimens trawled was about 13 inches long. *B. bigelowi* can be distinguished from Günther's species by the strong black pigment in the membrane that connects the lower rays of the upper part of the pectoral fin (colorless in *longifilis*), about 9 or 10 rays in the lower part of the pectoral fin (*cf.* 13), the greater length of the second anal ray, the gill-raker count (33–40 *cf.* 42), the presence of the large, conspicuous spots at the base of the caudal lobes, the general body coloration, and the relatively longer outer ventral and lower caudal rays.

Variability. Most of the known specimens are from a restricted area in the western Caribbean, and almost all others are old, shrunken and broken individuals. Therefore no attempt has been made to study the infraspecific variability of this species. However, two points are worthy of note. A juvenile specimen, 75.0 mm long, taken by the U.S. Fish and Wildlife Service vessel SILVER BAY in the Atlantic off central Florida (St. 454, 29°19′N, 79°58′W, 330 fms., USNM 156951) conforms to the diagnostic characters given above for *B.* (*B.*) *bigelowi*, but in certain morphometric features, such as its short head, it is notably different. No attempt can be made to study the relationships of this form until more specimens are caught. Secondly, a plot of the lengths of the ventral, pectoral and caudal fin rays against fish length shows a uniform and not unduly variable relationship, in contrast to the highly variable fin lengths in *B.* (*Hemipterois*) *viridensis* and, according to Garman (*13*: 257), in the Pacific *B.* (*Bathypterois*) *pectoralis* and *ventralis*.

Range. B. bigelowi is now known from the western Caribbean off Nicaragua and Costa Rica, from north of Puerto Rico and the Virgin Islands, off Monserat, from the Straits of Florida south of Tortugas, from the Atlantic off central Florida, and from the Gulf of Mexico. Since the only known specimens were caught in bottom trawls, it can be assumed that this species is a benthonic one. Its depth range, 260–400 fathoms, is shallower than that of most related species.

Synonyms and References:

Bathypterois longipes (*non* Günther), part, Goode and Bean, Smithson. Contrib. Knowl., *30*, 1895: 66 (juv. recorded from a Blake St.).

Bathypterois quadrifilis (*non* Günther) Longley and Hildebrand, Publ. Carnegie Inst. Wash., 535, 1941: 25 (S. of Tortugas, Florida).

Bathypterois bigelowi Mead, J. Wash. Acad. Sci., *48*, 1959: 366 (orig. descr., fig., Caribbean and Gulf of Mexico).

Bathypterois (*Bathypterois*) *longipes* Günther 1878

Figure 39

Study Material. Two specimens: 1, 171.6 mm SL, Albatross St. 2225, 36°05′ 30″N, 69°51′45″W, 2512 fms., Sept. 9, 1884, USNM 35635;[23] 1, 149.5 mm, Atlantis, SW. of the Azores, about 3800 m, Aug. 16, 1947.

Distinctive Characters. Body uniformly dark and without color pattern; fins colorless except for faint duskiness on the proximal third of the caudal lobes. Upper two rays of pectoral inseparably united basally, but separate distally, the point of separation posterior to the end of the base of the dorsal fin. Two or three rudimentary rays between these elongate upper pectoral rays and the lower pectoral fin. Lower pectoral fin with 9 or 10 rays, the lowermost not stronger than that above it. Scales beneath lower part of pectoral fin cycloid. Ventral rays eight, the outermost prolonged but failing to reach a vertical from adipose fin. Anal fin inserted in advance of end of base of dorsal fin; dorsal fin originating well behind axil of ventral fin. Eye minute, its horizontal diameter about half the depth of the posterior end of the maxillary.

Description. Proportional dimensions in per cent of standard length, based on the 171.6-mm specimen in the *Study Material*.

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[23] This specimen was reported and illustrated by Goode and Bean (*17*: 66, fig. 76). Most of their description was taken from Günther's account (*20*: 188). Goode and Bean included three juvenile specimens in their account: one, from a Blake St. (MCZ 27950), that should be referred to *B. phenax*; a second, from a Blake St. (USNM 47619), is *B. bigelowi*; and the third (USNM 31804), a Fish Hawk specimen incorrectly attributed to the Albatross collection, is a juvenile in very poor condition and probably referable to *B. phenax*.

Body: greatest depth 12.5; depth at origin of anal fin 11.5; greatest width 7.4.

Caudal peduncle: least depth 6.1.

Head: length 23.3.

Snout: length 8.0.

Eye: horizontal diameter 1.2.

Interorbital: width 7.5.

Premaxillary: length 16.6.

Dorsal fin: length of base 16.3.

Anal fin: length of base 10.3.

Distance from snout to origin of: dorsal fin 47.6; anal fin 59.5; ventral fin 38.4; pectoral fin 20.8.

Distance from: base of last dorsal ray to origin of adipose fin 18.4; adipose fin to upper procurrent caudal ray 17.5; base of last anal fin ray to ventral procurrent caudal ray 28.6; anus to insertion of ventral fin 14.9; anus to origin of anal fin 6.4.

Lateral-line scales: about 57.

Branchiostegal rays: 12.

Gill rakers: on first arch 11 + 1 + 29.

Fin rays: dorsal 15; anal 10; caudal I-16-II; ventral 8; pectoral—upper part 2 + 2 or 3, and lower part 9 or 10.

Vertebrae: 54, including urostyle.

Body compressed, snout depressed, the body deepest under dorsal fin origin, this depth 1.9 in hl; depth at anal origin 1.9 in head. Least depth of Caudal peduncle 3.8 in head. Scales present on cheeks, body and bases of caudal lobes; almost all missing in the single study specimen; scales beneath lower part of pectoral fin cycloid.

Head 4.3 in SL, nearly flat above and before eye. Snout rounded anteriorly. Eye minute and horizontally elliptical; its greatest diameter about 7 in length of snout or about half the depth of posterior end of maxillary. A horizontal series of pores below eye; top of snout pierced by sensory pores as well as by the nostrils. Olfactory organ large; the membrane separating the anterior from the posterior nostril bears a short flap. Interorbital 3.1 in hl. Branchiostegal membranes broad, extending beyond opercles posteriorly but not reaching bases of lower pectoral fin rays.

Gill rakers flattened and bearing spines along the inner edge; longest raker on first arch about twice the length of the opposite gill filament.

Teeth minute and forming a narrow band on lower jaw, the band becoming broader anteriorly. Premaxillary teeth similar. A few small palatine teeth. Vomer toothless.

Dorsal fin inserted well behind axil of ventral fins; predorsal distance 2.1 in SL; first 2 rays simple, the rest branched, the last divided to its base. Anal fin inserted well in advance of end of base of dorsal; preanal distance 1.7 in SL; only the first ray simple, the last ray divided to its base; distance from last ray to procurrent ventral caudal rays 3.5 in SL. Caudal fin with 2 lower rays slightly prolonged. Ventral fin with 2 outermost rays simple and produced but failing to reach a vertical from adipose fin. Preventral distance 2.6 in SL.

Pectoral fin with the elongate uppermost 2 rays fused basally but separate distally, the point of separation posterior to end of base of dorsal fin; 2 or 3 short rudimentary rays between them and the lower part of fin; 9 or 10 rays in lower part, the lowermost not stronger than that above it, the rays nearly equal in thickness (all broken on study specimen). Prepectoral distance 4.8 in SL.

Color. In alcohol, body uniformly dark and without pattern; this specimen dark brown, with each scale pocket outlined by a pigmentless margin. Bases of caudal lobes dusky, but without the black spots characteristic of the related *B. bigelowi*; the remaining fins colorless. Eye, opercular lining, branchiostegal membrane, and pharyngeal and abdominal linings black.

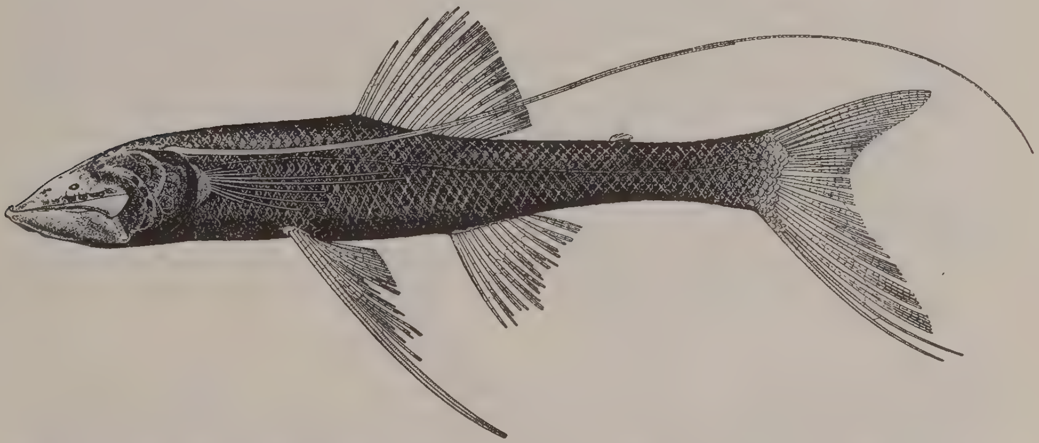

FIGURE 39. *Bathypterois* (*Bathypterois*) *longipes*, 149.5 mm long, from southwest of the Azores, ATLANTIS, about 3800 m, Aug. 16, 1947, MCZ 36634. Drawn by Margaret G. Bradbury.

Remarks. Nothing is known of the biology of this deep-water species. It appears to be one of the more common species encountered at depths greater than 4000 m.

Relationship. B. longipes is the most closely related to the shallower-water *B. bigelowi.* Differences between the two are noted in the diagnoses. Parr (*29*: 26) considered the Pacific *B. longicauda* Günther to be a synonym of *longipes.* The question was further discussed by Nybelin (*28*: 254), who re-examined the type of *longicauda* and suggested that it is a teratological specimen.

Because of the inadequate descriptions and subsequent loss of the type specimens of the South African species, no attempt is made here to compare *B. longipes* with these. It appears to be similar in many respects to *B. capensis* Gilchrist and von Bonde (*16*: 8, pl. 2, fig. 1).

Variability. Available material does not permit a study of the variability within this species. The adult specimens studied agree well with the account of the abundant eastern Atlantic material provided by Nybelin (*28*: 256), who also discussed the variation in fin length and other characters.

Range. B. longipes is known from deep water in the South Atlantic off the coast of

Brazil (the type locality), off New England,[24] and from several eastern Atlantic localities.[25] Bathymetric range: 2512–5610 m.

Synonyms and References:

Bathypterois longipes Günther, Ann. Mag. nat. Hist., (5) *2*, 1878: 184 (orig. descr.; E. coast of S. America, Challenger, 2650 fms.); Anon., Rep. sci. Res. 'Challenger', Narrative *1* (1), 1885: 217, fig. B (descr. from Günther, 1878); Günther, Rep. sci. Res. 'Challenger', Zool., *22*, 1887: 188, pl. 48, fig. A (descr., figs. incl. dorsal view of head); Vaillant, Expéd. Sci. 'Travailleur' 'Talisman', Poiss., 1888: 134 (in key); Garman, Mem. Mus. comp. Zool. Harvard, *24*, 1899: 400 (range); Regan, Ann. Mag. nat. Hist., (8) *7*, 1911: 127 (in key); Murray and Hjort, Depths of Ocean, 1912: 416 and elsewhere (distr.); Koefoed, Rep. 'Michael Sars' N. Atlantic Deep Sea Exped., *4* (1), 1927: 63 (descr., distr., 2 spec. from Michael Sars St. 53: 34°59′N, 33°01′W, 2615 m); Parr, Bull. Bingham oceanogr. Coll., *3* (3), 1928: 26 (in key, diagn.); Fowler, Bull. Amer. Mus. nat. Hist., *70* (1), 1936: 357, fig. 170 (descr. from Günther, 1887); Grey, Fieldiana: Zool., *36* (2), 1956: 133 (distr., refs.); Nybelin, Internat. Union Biol. Sci., (B) 16, 1954: 70 (Swedish Albatross spec. listed); Nybelin, Rep. Swedish Deep Sea Exped., 2 (Zool.) *20*, 1957: 254, pl. 1, fig. 1 (E. Atl., descr., distrib., and abund. reviewed); Hansen and Wingstrand, 'Dana' Rep., 54, 1960: 8 (exceptionally large erythrocytes – 20×15 μ).

Bathypterois sp. Vaillant *in* Roule, Résult. Camp. Sci. Monaco, *52*, 1919: 130 (juv. ident. by Nybelin, 1957: 255).

Bathypterois (*Synapteretmus*) *longipes*, Goode and Bean, Smithson. Contrib. Knowl., *30*, 1895: 66, pl. 20, fig. 76 (adult only = *B. longipes*; descr.); Jordan and Evermann, Bull. U.S. nat. Mus., *47* (1), 1896: 546 (descr., from Goode and Bean, 1895, and Günther, 1887); Jordan and Evermann, Rep. U.S. Comm. Fish (1895), App. 5, 1896: 298 (listed).

Negative References:

Bathypterois longipes of Filhol, La Vie au Fond des Mers, 1885: 92, fig. 30 (? = *B. dubius* Vaillant).

Bathypterois longipes, part, of Goode and Bean, Smithson. Contrib. Knowl., *30*, 1895: 66 (adult, figured, = *B. longipes*; juv., USNM 31804 and MCZ 27950, = *B. phenax* Parr; juv. from a Blake St. = *B. bigelowi* Mead).

Bathypterois longipes of Briggs, Bull. Florida State Mus., Biol. Sci., *2* (8): 258 (listed, based on Goode and Bean, 1895, juveniles).

Bathypterois (*Bathypterois*) *phenax* Parr 1928

Figure 40

Study Material. Three specimens: the type, 160.0 mm SL, Pawnee St. 54, 21°16′N, 71°18′W, 900–945 fms., Dec. 4, 1927, BOC 2133; 2, 125.0 and 84.3 mm, Oregon St. 1303, 28°47′N, 87°50′W, 1150–1200 fms., May 26, 1955, CNHM 64078.

Distinctive Characters. Body uniformly dark, without conspicuous color pattern. Upper two rays of pectoral fin firmly united basally, dividing at a point beyond origin of dorsal fin; the rays elongate. One to four rudimentary rays between these elongate upper pectoral rays and lower pectoral fin. Lower ray of lower pectoral fin not notably long or strong. Scales beneath lower part of pectoral fin cycloid. Nine rays in ventral fin, the outer longest but failing to reach a vertical with adipose fin. Two lowermost principal caudal rays unbranched. Subcaudal notch (formed by ventral procurrent caudal rays) present. Eye intermediate in size between that of *B. quadrifilis* and *B. longipes* or *B. bigelowi*, its vertical diameter slightly less than greatest breadth of maxillary. Adipose fin closer to end of base of dorsal fin than base of caudal.

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[24] Albatross St. 2225 (see *Study Material*, p. 133) and Atlantis St. 15, 35°37′N, 30°51′W, Aug. 16, 1947, MCZ 36634.

[25] Nybelin (*28*: 254) and Grey (*18*: 133) have reviewed the deep-abyssal records of this species. Nybelin quite rightly questioned the identity of the juveniles, from much shallower water, that were reported by Goode and Bean (*17*: 66). Three of these have been re-examined and none is *B. longipes* (see ftn. 23, p. 133).

Description. Proportional dimensions in per cent of standard length, based on the two larger study specimens, 160.0 and 125.0 mm.

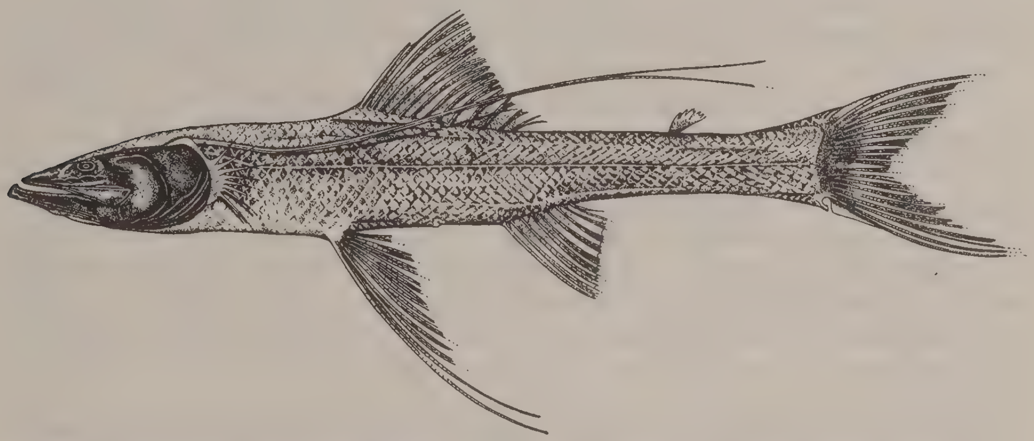

FIGURE 40. *Bathypterois* (*Bathypterois*) *phenax*, 160 mm long, from off the Bahama Islands, PAWNEE St. 54, 900–945 fms., BOC 2133, holotype. Drawn by Mildred H. Carrington.

Body: greatest depth 15.1, 11.7; depth at origin of anal fin 12.4, 10.0; greatest width 8.6, 7.9.

Caudal peduncle: least depth 7.9, 6.8.

Head: length 24.1, 23.0.

Snout: length 7.4, 8.3.

Eye: horizontal diameter 1.6, 1.8.

Interorbital: width 8.1, 8.5.

Premaxillary: length 14.1, —.

Dorsal fin: length of base 16.7, 14.5.

Anal fin: length of base 9.1, —.

Distance from snout to origin of: dorsal fin 43.2, 42.6; anal fin 61.0, 60.8; ventral fin 39.6, 38.6; upper pectoral ray 19.9, 19.4.

Distance from: base of last dorsal ray to insertion of adipose fin 19.8, 22.3; insertion of adipose fin to dorsal procurrent caudal rays 19.4, 20.3; base of last anal ray to ventral procurrent caudal ray 29.9, 31.3; insertion of ventral fin to origin of anal fin 21.3, 22.2; anus to insertion of ventral fin 12.4, 14.5; anus to origin of anal fin 8.8, 8.5.

Lateral-line scales: about 54.

Branchiostegal rays: 12 or 13.

Gill rakers: on first arch 10–12 + 1 + 27–28.

Fin rays: dorsal 14 or 15; anal 9; caudal I-16-II; ventral 9; pectoral—upper part 2 + 1–4 and lower part 7 or 8.

Vertebrae: 54, including hypural (type only).

Body compressed, snout depressed, the body deepest at dorsal origin, its depth about twice its width at this point, its greatest depth 1.6 and its depth at anal origin 1.9–2.3 in head. Least depth of the compressed Caudal peduncle 3.0–3.4 in hl. Scales present on cheek, body and base of caudal fin, the scales cycloid and deciduous (almost all missing in the three study specimens), those beneath lower part of pectoral fin cycloid also. Lateral line complete, originating above the uppermost pectoral ray and possibly terminating at caudal base.

Head 4.1–4.3 in SL, nearly flat above and before eye. Snout flat above, depressed, rounded anteriorly; its length 3.3 in hl. Eye minute, horizontally elliptical, and laterally directed, its diameter 4.5–4.7 in length of snout, its vertical diameter slightly less than greatest breadth of maxillary. A horizontal row of sensory pores below eye; top of snout pierced by several sensory pores as well as by the nostrils and covered anteriorly by small papillae. The anterior Nostril smaller than the posterior; a short flap on the membrane separating the two. Interorbital 2.7–3.0 in hl. Opercular bones poorly ossified. Branchiostegal membrane broad, joined near tip of lower jaw but free from isthmus, extending rearward beyond opercles to base of lower pectoral fin.

Gill rakers present on all four arches, those on anterior arch flattened and longer than the opposing gill filaments; each raker with a row of spines along its inner edge.

Outer surfaces of the Mandible pierced by series of pores. Premaxillary 1.7 in hl. Maxillary surmounted by a slender supramaxillary that extends forward to beneath eye.

Teeth. A narrow band of minute teeth on lower jaw. On premaxillary, a broader band of similar teeth. A small patch on vomer. Palatine, symphysis of each jaw, and tongue toothless.

Dorsal fin inserted close behind a vertical from bases of inner ventral rays; predorsal distance 2.3 in SL; the first ray simple, the others divided, the last split to its base. Adipose fin closer to end of dorsal base than to base of caudal. Anal fin inserted slightly behind a vertical from last dorsal ray, its first ray simple, the rest branched; preanal distance 1.6 in SL. Distance from last anal ray to ventral procurrent caudal ray about 3.3 in SL. Caudal fin with a subcaudal notch (formed by ventral procurrent caudal rays); the two lowermost principal rays unbranched. Caudal fin with last ventral procurrent ray separated from first lower principal ray by a notch, the procurrent ray bent upward to form a hook. Ventral fin with the outer 2 rays simple, united at their bases, and somewhat prolonged, reaching end of base of anal fin or, in the larger specimen, slightly beyond; preventral distance 2.5–2.6 in SL.

Pectoral fin with upper 2 rays elongate, stiffened throughout, firmly united basally and joined for most of their length but separate distally, dividing at a point beyond origin of dorsal fin; these rays extending well beyond base of caudal fin in the smallest specimen (84.3 mm) and to the caudal base in the largest. A variable number (1–4) of short rudimentary rays between these rays and the lower part of the fin; 3 or 4 of them in the juvenile, 1 or 2 in the adults. Distance from snout to base of upper ray 5.0–5.2 in SL. The lower part of fin, broken in all available specimens, composed of 7 or 8 well-developed rays, none much heavier than the others, the lower one not notably long or strong.

Color. In alcohol, all of the three specimens are dark, the pattern mottled, the pigment stronger in each scale pocket. The 125-mm fish shows some evidence of vertical cross-banding on one side, but this may be the result of differential abrasion during capture. The juvenile is much darker than the adults. All fins dusky; the ends of the prolonged rays a hyaline white. Cheeks and pharyngeal and abdominal cavities black.

In fresh specimens, body black except for the white edges of the scale pockets. The dorsal fin, especially the distal half of the rays themselves, dusky; the ventral and anal fins, especially the distal parts, also dusky; the caudal fin black. Iris of eye greenish.

Size. The largest known individual is the 160-mm type. Since the species is known from but few individuals, nothing further can be said of the biology of this species.

Relationships. Following the original description of *Bathypterois atricolor phenax*, Parr (*29*: 30) noted the general similarity between this species and four other nominal forms: *B. atricolor* Alcock; *B. ventralis* Garman, eastern tropical Pacific (*13*: 256, pl. 55, fig. 1); *B. antennatus* Gilbert, Hawaii (*14*: 590); and *B. atricolor indicus* Brauer, western Indian Ocean (*10*: 144). Parr then noted that these five forms might equally well be considered species or subspecies. I concur wholly with this view, and would add two additional named forms to this complex: *B. dubius* Vaillant, eastern Atlantic (*35*: 124; *12*: 105); and *B. pectoralis* Garman, eastern tropical Pacific (*13*: 257, pl. K, fig. 1).

The status of *B. dubius* is uncertain. Vaillant based his description on 70 specimens from the eastern tropical Atlantic. A type specimen was designated but not described by Bertin and Estève (*9*), but Grey (*18*: 131) has noted that this fish, from TALISMAN St. 128, was not included in the material or localities given in the type account. She has also pointed out (*18*: 110, ftn. 1) that the data given by Vaillant seldom agree with those later published by Smith (*34*: 869). Three of the original Vaillant specimens were sent to the United States by the Paris Museum. Unfortunately these three[26] differ from Vaillant's account in dorsal fin-ray count (16 *cf.* 14 in Vaillant's figure; "1, 14" in text), in horizontal diameter of eye (larger in the described specimens), and in form of the anterior edge of the subcaudal notch. It is likely that there is more than a single form, species or subspecies, represented in the original series. A study of these cannot be attempted here. *B. dubius* is usually separated from its congeners by the more posterior placement of its anal fin, the origin of which is well separated from the vertical of the last dorsal ray.

Fin placement, especially that of all unpaired fins, appears to be somewhat variable geographically though more or less constant within samples from any specific locality. Anal fin placement may be a valid character for the separation of *B. phenax*, but in most other respects it is closely allied to its eastern Atlantic counterpart, *B. dubius*.

It is difficult to interpret differences between Garman's eastern Pacific *B. pectoralis* and *B. ventralis* because of the differences in size of the two type series. Both can be separated from *B. dubius* (as represented by the three available Vaillant specimens) by the dorsal fin-ray count (12–14 *cf.* 14 or 16 in *dubius*); ventral fin ray count (9 *cf.* 8); rays in lower part of pectoral (11–13 *cf.* 10 or occasionally 11); position of anus (ventral-origin-to-anus divided by anus-to-anal-origin 1.4–1.9 in *pectoralis* and *ventralis*; 1.2–1.3 in *dubius*); and anterior extent of the supramaxillary, which extends forward to beneath the posterior edge of the eye in *dubius* but does not reach the eye in either *ventralis* or *pectoralis*.

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[26] MCZ 27605 (1 specimen) and USNM 42087-8 (2 specimens).

B. ventralis can be separated from *pectoralis* as follows: lower pectoral rays 12–13 (11–12 in *pectoralis*); dorsal fin 12 (*cf.* 13–14); center of anus to origin of anal fin 7.1–8.3 % of SL (*cf.* 8.2–9.9 %); and width of interorbital 9.0–9.1 % of SL (*cf.* 7.9–8.1 %).

The shallower snout and caudal peduncle and the position of the adipose fin separate the Hawaiian *B. antennatus* immediately from its congeners. The adipose fin is much closer to the bases of the upper principal caudal rays than to the end of the dorsal base, its post-adipose distance being less than the length of the base of the dorsal fin.

No material from the Indian Ocean is available, and the single specimens from various western Pacific localities[27] differ among themselves and from the named forms. The characterization of these cannot be attempted here, and their naming is futile in the absence of any information regarding their distribution, reproduction and speciation.

Range. Adults of *B. phenax* are now known from five western Atlantic localities; one north of Haiti at 900–945 fathoms, another from the Gulf of Mexico south of Mississippi, 1150–1200 fathoms (see *Study Material*), and two others from the Gulf of Mexico.[28] Juveniles have been caught in the Gulf of Mexico north of western Cuba at 955 fathoms,[29] and off New Jersey at 452 fathoms,[30] and another was recently caught in the central Gulf.[31]

Synonyms and References:

Bathypterois (*Synapteretmus*) *longipes* (*non* Günther), part, Goode and Bean, Smithson. Contrib. Knowl., *30*, 1895: 68 (juv., Blake and Fish Hawk coll.; USNM 31804, MCZ 27950).

Bathypterois atricolor phenax Parr, Bull. Bingham oceanogr. Coll., *3* (3), 1928: 31 (orig. descr., off the Bahamas, *cf. B. atricolor indicus*, *B. antennatus* and *B. ventralis*); Shanklin, Acta Zool., Stockholm, *15*, 1934: 409, figs. 6–8 (anat. of cerebellum; notes smallness of optic tectum and tractus mesencephalo-cerebellaris anterior); Shanklin, Philos. Trans., London, (B) *224*, 1935: 361, figs. 12–19 (brain anat., again notes atrophied optic system, p. 396).

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[27] USNM 149778 (Japan); USNM 149654 (Japan); USNM 135401 (Molucca Passage); USNM 135399 and 135400 (Philippines); all cataloged as *Bathypterois atricolor*. Matsubara (*23*) has recorded a specimen from Japan as *B. atricolor antennatus*. This fish differs from Gilbert's types of *B. antennatus* in depth of caudal peduncle, placement of adipose fin, number of gill rakers, fin-ray lengths, and other characters.

[28] Oregon St. 2574, 26°34′N, 89°53′W, 1450 fms., July 28, 1959; and Oregon St. 2577, 27°48′N, 88°45′W, 850–1100 fms., July 30, 1959.

[29] Reported as *B. longipes* by Goode and Bean (*17*: 66), Blake St. CCXLVI, MCZ 27950.

[30] Reported as *B. longipes* by Goode and Bean (*17*: 66), the specimen erroneously attributed to the Albatross rather than to the Fish Hawk collection, 39°29′N, 72°01′W, 425 fms., USNM 31804.

[31] A 95.5-mm specimen from Oregon St. 2821, 28°47.5′N, 87°57′W, 1000–1100 fms.

Bathypterois atricolor, Fowler, Monogr. Acad. nat. Sci. Philad., *6*, 1944: 438 (listed, from Parr, 1928).

Bathypterois phenax, Grey, Fieldiana: Zool., *36* (2), 1956: 133 (distr.); Briggs, Bull. Florida State Mus., Biol. Sci., *2* (8); 1958: 257 (listed, misspelled *phenae*). Grey, Fieldiana: Zool., *39* (16), 1958: 162 (fig. and descr., two spec. from Oregon St. 1303).

Bathypterois (*Bathypterois*) *quadrifilis* Günther 1878

Figure 41

Study Material. Twenty-one specimens, 95.5–149.5 mm, all from the tropical western Atlantic: 11, 115.0–149.5 mm, Oregon St. 1426, 29°07′N, 87°57′W, 600 fms., Sept. 24, 1957, in USNM, MCZ, TU, and CNHM; 2, 120.5 and 124.5 mm, Oregon St. 1955, 16°48′N, 82°33′W, 550 fms., Sept. 17, 1957, CNHM 64438; 2, 144.5 and 146.5 mm, Harvard-Havana Exped., Atlantis St. 2996, 23°22′N, 81°05′W, 470–665 fms., March 16, 1938, MCZ 35598; 1, 129.0 mm, Blake St. 257, off Grenada, 553 fms., MCZ 27927; 3, 126.0–129.5 mm, Blake St. 98, off St. Vincent, 573 fms., MCZ 27925; 1, 124.5 mm, Albatross St. 2117, 15°24′40″N, 63°31′30″W, 683 fms., Jan. 27, 1884, USNM 34963; 2, 95.5 and 129.5 mm, Albatross St. 2385, 28°51′N, 88°18′W, 730 fms., March 3, 1885, USNM 44326, SU 9547.

Distinctive Characters. Body black or nearly black, the scale pockets with white borders. Fins black. Upper two pectoral rays united basally, separate distally, the point of separation being anterior to a vertical from ventral fin origin, much farther forward than in most related species. Usually only one lower ray in upper part of pectoral fin; this ray small and not enclosed in a fin membrane. Nine or ten lower pectoral rays, the lowest long and strong, its base much thicker than the ray adjacent to it. Scales beneath lower part of pectoral fin strongly pectinate, more adherent than the cycloid body scales farther back. Eye relatively large, its horizontal diameter much greater than the greatest depth of the maxillary with its supramaxilla. Subcaudal notch present,[32] formed by the posterior ventral procurrent caudal rays. Two outer ventral rays elongate. Nine rays in ventral fin. Lower caudal lobe little if any longer than upper, the lower simple rays not greatly prolonged. Vertebrae 57 or more.

Description. Proportional dimensions in per cent of standard length, based on five specimens, 115.0–149.5 mm SL, from Oregon St. 1426, Gulf of Mexico, 600 fms.; see *Study Material.*

Body: greatest depth 13.2–15.6; depth at origin of anal fin 12.5–13.4; greatest width 7.3–8.5.

Caudal peduncle: least depth 8.2–8.8.

Head: length 19.7–21.4.

Snout: length 6.2–7.1.

Eye: horizontal diameter 2.2–2.7.

Interorbital: width 7.0–8.1.

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[32] *B. quadrifilis* was not described as having a subcaudal notch by either Günther (*20*: 189, pl. 33, fig. B) or by Goode and Bean (*17*: 65, fig. 75). Both of these accounts are in error in this respect. Goode and Bean's specimens, now in the U.S. National Museum, have distinct subcaudal notches, and Dr. N. B. Marshall has generously re-examined Günther's types in my behalf and has written: "*Bathypterois quadrifilis* Günther. I have looked at the types (*B.M.* Reg. No. 1887 12.7.199–20) and find both to have a distinct subcaudal notch".

Premaxillary: length 12.6–13.8.

Dorsal fin: length of base 13.8–14.5.

Anal fin: length of base 7.3–8.3.

Distance from snout to origin of: dorsal fin 41.8–43.7; anal fin 57.5–59.7; ventral fin 37.7–39.5; upper pectoral fin 16.2–18.3.

Distance from: base of last dorsal ray to insertion of adipose fin 18.1–21.3; adipose origin to base of upper procurrent caudal rays 21.2–23.8; base of last anal ray to lower procurrent caudal 30.6–32.2; anus to insertion of ventral fin 12.3–14.4; anus to origin of anal fin 5.5–7.4.

Lateral-line scales: about 60.

Branchiostegal rays: 12 or 13 (infrequently 11).

Gill rakers: on first arch 12 or 13 + 1 + 27–30 = 40–43.

Fin rays: dorsal 14 or 15; anal 9 or 10; caudal I-16-II; ventral 9; pectoral—upper part 2 + 1 and lower part 9 or 10 (occasionally 11).

Vertebrae: 57 or 58 (infrequently 59).

Body compressed, snout depressed, the body deepest under origin of dorsal fin, this depth 1.3–1.6 in hl; depth at anal origin 1.5–1.7 in head; greatest width 1.6–2.0 in greatest depth. Least depth of Caudal peduncle 2.3–2.6 in hl. Scales present on cheek, body and base of caudal fin, the scales that extend onto caudal lobes usually lost during capture; most body scales cycloid, their edges irregular; scales beneath lower part of pectoral fin strongly pectinate, more adherent than the cycloid body scales farther back, the finger-like projections, usually about 5 in number, as long as the diameter of the scale in adults, shorter in juveniles; a row of narrow and elongate scales along bases of dorsal and anal fins. Adipose fin, although well developed, almost obscured in some specimens by the mid-dorsal scales that precede it. Lateral line beginning at upper end of gill opening and ending on caudal fin above the center ray; the scales cycloid and bearing a simple tube.

Head 4.6–5.1 in SL, more or less flattened above and before eye. Snout 2.9–3.3 in head. Eye small, but considerably larger than that of most bathypteroid species, its greatest diameter greater than the greatest depth of the maxillary with its supramaxillary, 2.5–3.3 in snout; Lens and Pupil slightly longer than high, more than half the horizontal length of the eye. Two longitudinal rows of pores on top of head, another row below each eye. Olfactory organ well developed, a short flap on the membrane separating the anterior from the posterior nostril. Interorbital 2.6–2.8 in hl. Branchiostegal membranes well developed, the supporting rays strong, the membranes joined to one another anteriorly, and extending posteriorly but a short distance beyond operculum. Branchiostegal rays 12, or infrequently 11, 5 or 6 originating on the epihyal.

Gill rakers on first arch well developed, flattened, and bearing spines along their inner edges. The rakers near the angle of the arch considerably longer than the opposing gill filaments, those on the successive gill arches shorter.

Mandible broad and heavy, pierced along its lower outer surface by a row of 6–8 pores. Lower jaw terminal; symphysial knob well developed. Maxillary 1.5–

1.6 in hl, broad, surmounted by an elongate supramaxillary which terminates anteriorly under the rear edge of the eye.

TEETH. A narrow band of minute teeth on mandible; a broader band of similar teeth on premaxillary; and occasionally a very small patch of minute teeth behind vomerine knob or a few microscopic tooth-like structures on palatine. Vomer and palatine usually toothless, symphysis of each jaw and the very small tongue always so.

DORSAL fin inserted well behind axil of ventral fin; predorsal distance 2.3–2.4 in SL; the first 2 rays simple, the rest branched, the last usually to its base; length of base 1.4–1.5 in hl. ADIPOSE fin well developed, somewhat less broad than in many other *Bathypterois* (*e. g. B. phenax*); its position between dorsal and caudal fins variable. Distance from base of last dorsal ray to insertion of adipose 4.7–5.5 in SL. ANAL fin inserted under, or slightly behind, base of last dorsal ray; preanal distance about 1.7 in SL; length of base 2.5–2.8 in head. First ray simple, the rest branched, the last divided to its base; the 3rd ray longest, but little if any longer than the 2nd or 4th; distance from last anal ray to ventral procurrent caudal ray 3.1–3.3 in SL. CAUDAL fin with lower rays simple and somewhat prolonged, the lower lobe but slightly longer than the upper. Subcaudal notch present, formed by the posterior ventral procurrent fin ray. VENTRAL fin with 2 outer rays simple, united basally, and elongate, usually ending somewhere under base of anal or somewhat beyond. Preventral distance 2.5–2.7 in SL.

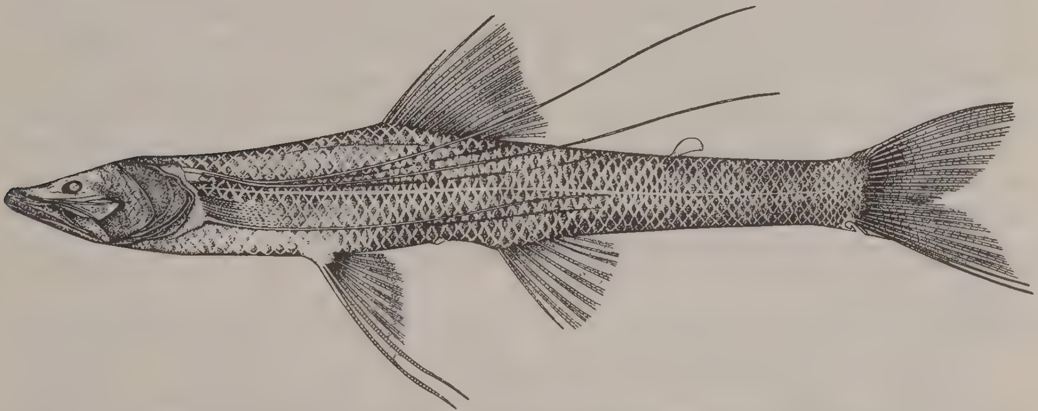

FIGURE 41. *Bathypterois* (*Bathypterois*) *quadrifilis*, a composite drawn from a series of specimens 121–142 mm long, from the Gulf of Mexico south of Mississippi, OREGON St. 1426, 600 fms. Drawn by Mildred H. Carrington.

PECTORAL fin inserted behind upper end of gill opening; prepectoral distance 5.5–6.2 in SL. Upper 2 rays of upper part united basally, separate distally, the point of bifurcation farther forward than in most bathypteroid species, always in advance of origin of dorsal fin and usually ahead of that of ventral fin; these upper rays stiffened and recurved upward. Usually only one small rudimentary ray in upper part below the 2 rays, not enclosed in a fin membrane. Lower part of pectoral fin with 9 or 10 rays, all well developed (all rays broken in all available specimens), lowermost ray long and strong, about twice as thick basally as its neighbor, stiffened and curved upward, and extending to or beyond base of caudal.

Color. In alcohol, black or very dark brown, the edges of the scale pockets white. Opercles, branchiostegal membranes, and pharyngeal and abdominal linings black. Dorsal and anal fins black, the proximal part of the interradial membrane less heavily pigmented. Ventral fin and lower pectoral fin dusky; adipose fin clear; caudal black.

Relationships. B. quadrifilis is the most closely related to the Pacific *B. pectinatus* Mead, which is known only from one specimen taken by the ALBATROSS at St. 4654,[33] and another by the VEMA.[34] This species is in turn related to *B. ventralis* Garman, an eastern Pacific representative of the *atricolor-phenax* complex (see p. 139).

Range. The types of *B. quadrifilis* were collected in the South Atlantic off the coast of Brazil, CHALLENGER Sts. 121 and 126 (500 and 770 fms.). All other known specimens are listed above under *Study Material.* These came from depths of 470–665 fathoms in the northeastern Gulf of Mexico, north of Cuba, the western Caribbean off Nicaragua, and off Grenada and St. Vincent in the British West Indies.

Synonyms and References:

Bathypterois quadrifilis Günther, Ann. Mag. nat. Hist., (5) *2*, 1878: 184 (orig. descr., CHALLENGER, coast of Brazil, 770 fms.); Günther, Rep. sci. Res. 'Challenger', Zool., *22*, 1887: 189, pl. 33, fig. B (descr.; figs. incl. ventral view and special scales); Agassiz, Bull. Mus. comp. Zool. Harvard, *15* (Three Cruises of the BLAKE) (2), 1888: 32, fig. 217 (orig. fig., no data or descr.); Vaillant, Expéd. Sci. 'Travailleur' 'Talisman', Poiss., 1888: 134 (in species key); Garman, Mem. Mus. comp. Zool. Harvard, *24*, 1899: 257, 400 (*cf.* Pacific *B. pectoralis* Garman; range); Regan, Ann. Mag. nat. Hist., (8) *7*, 1911: 127 (in key); Parr, Bull. Bingham oceanogr. Coll., *3* (3), 1928: 27 (in key; diagn.).

Bathypterois (*Synapteretmus*) *quadrifilis*, Goode and Bean, Smithson. Contrib. Knowl., *30*, 1895: 65, pl. 20, fig. 75 (descr.); Jordan and Evermann, Rep. U.S. Comm. Fish. (1895), App. 5, 1896: 298 (listed); Jordan and Evermann, Bull. U.S. nat. Mus., *47* (1), 1896: 545 (descr.; from Goode and Bean, 1895); Jordan, Stanford Univ. Publ., Univ. Ser., Biol. Sci., *3* (2), 1923: 154 (type of *Synapteretmus*); Jordan, Evermann and Clark, Rep. U.S. Comm. Fish (1928), App. 10, 1930: 166 (listed).

Negative Reference:

Bathypterois quadrifilis, Longley and Hildebrand, Publ. Carnegie Inst. Wash., 535, 1941: 25 (= *Bathypterois bigelowi* Mead).

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[33] Pacific off Point Aguja, Peru, 5°46′S, 81°32′W, 1036 fms., Nov. 12, 1904. *B. pectinatus* is similar to the Atlantic *B. quadrifilis* in many characters, the most notable being the strongly pectinate scales beneath the lower part of the pectoral fin and the anterior point of separation of the two upper elongated pectoral rays. This latter character is also typical of *B. ventralis*. It differs from the Atlantic *quadrifilis* in the thickness of the lowermost pectoral ray, which, although elongate, is not notably thicker proximally than its neighbor, its colorless caudal fin, less deep abdomen and caudal peduncle, smaller eye and longer snout, more anteriorly situated dorsal fin, and more posterior adipose relative to dorsal and caudal fins.

[34] VEMA St. SBT 37, Panama Bay, 05°00′N, 79°04′W, Nov. 15, 1958, 940 fms., AMNH 20401.

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Family Bathysauridae

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Characters. MODERATELY SLENDER DEEP-SEA BOTTOM FISHES WHICH GROW TO A LENGTH OF ABOUT TWO FEET. Body compressed, especially posteriorly. Head and snout depressed. Eye of moderate size and horizontally elliptical, dorsolaterally directed, entering into dorsal profile. Pupil not keyhole-shaped but elliptical and with a prominent lensless space. Interorbital space broad, bony, and slightly concave. Supraorbital bone fused to skull or completely absent.

Scales present on cheeks, opercles, body, and base of caudal fin, the few scales remaining on the available study specimens cycloid and with smooth free edges; top of head without scales; scales on operculum not notably larger than those elsewhere. Lateral line complete, terminating at base of caudal fin or continuing onto lower lobe of caudal fin.

Dorsal fin originating in second quarter of body length, its base somewhat shorter or slightly longer than length of head, the fin composed of about 15–18 rays. Anal fin originating behind posterior end of base of dorsal fin, its base shorter than length of premaxillary, the fin formed of 11–14 rays. Caudal fin with a shallow fork, the lobes approximately equal, the fin with 19 (1-17-1) principal rays. Ventral fins inserted below, or anterior to, origin of dorsal fin, in anterior third of body, and with truncated edges, the fin lying in a horizontal plane when expanded and formed of 8 rays (the outermost may represent 2 fused rays). Pectoral fin inserted below middle of side of body, undivided, formed of 15–17 rays, the central ray or rays usually somewhat prolonged and branched or unbranched. Adipose fin present or absent, situated over posterior end of base of anal fin when present.

Anus immediately anterior to origin of anal fin. A small anal papilla present.

No luminous organs.

Lower jaw terminal, the mandible lying partly outside of the mouth, both laterally and anteriorly, when the mouth is closed. Premaxillary long, thin, toothed, and firmly

Reprinted from Memoir Sears Foundation for Marine Research, I (5), 1966: 103–113.

attached to the skull anteriorly. Maxillary completely absent or indistinguishably fused with the premaxillary or the palatine. No supramaxillary bone. Vomer U-shaped, continuous with, and firmly bound to, the palatines.

Free tip of tongue short and blunt, the part supported by the glossohyal bound to that formed by the urohyal in an oblique position.

Teeth present on jaws, vomer and palatines, pharyngeals, and tongue; the teeth needle-like, recurved, and barbed, of variable size, but no enlarged canine or lanceolate teeth; outer row of palatine teeth fixed but all others depressible.

Gill arches extending far forward into the mouth, past the angle of the gape. Gill rakers reduced to patches of spines on the arches. Pseudobranchiae well developed, located high in gill cavity, and not covered by skin. Branchiostegal membranes fleshy and broad, joined to one another and to the isthmus near the tip of the lower jaw, extending posteriorly beyond opercular flap. Branchiostegal rays 8–13. Opercular flap covered by skin and flesh, the underlying bones thin, incomplete, and greatly reduced, its posterior margin formed by both the opercular and the subopercular bones.

Remarks. The bathysaurids have been variously included within the Synodontidae and the Harpadontidae, fishes to which they are certainly closely related. The three families are currently recognized, and there can be little doubt that *Bathysaurus* and *Harpadon* descended from ancestors that resembled the lizardfishes. Both have the specialized gill rakers and dentition suggestive of certain synodontids. *Bathysaurus*, however, is adapted for life on the bottom, while the harpadontids are midwater marine and estuarine species. In *Bathysaurus*, the head is depressed, the eyes are well back from the snout and directed dorsolaterally, the head and body heavy, and the bones well ossified. The head and body of *Harpadon* are compressed and of lighter construction and the eyes are anteriorly placed and directed forward.[1] These structural modifications have produced two groups vastly different in appearance.

Nothing is known of the development, life history, or anatomy of any bathysaurid species.

Size. The bathysaurids reach a larger size than most deep-water inioms. The adults frequently exceed two feet in length.

Range. Widespread, although uncommonly taken, in deep water (below about 900 fms.).[2] Not yet taken in the Indian Ocean.

Genera. The family contains only the genus *Bathysaurus*.

Genus *Bathysaurus* Günther 1878

Bathysaurus Günther, Ann. Mag. nat. Hist., (5) *2*, 1878: 181; type species, *Bathysaurus ferox* Günther 1878, designated by Jordan and Evermann, Bull. U.S. nat. Mus., 47 (1), 1896: 539; east coast of New Zealand at 1100 fms.

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[1] Since no harpadontids are known from the Atlantic, no further account of the group will be found in these volumes. The most celebrated species is *H. nehereus*, which is caught in the estuaries of the large Indian rivers and which, in dried form, is the delicacy known as "Bombay Duck." For further information on the family, see: Günther (*4*: 180, for the bathypelagic *H. microchir*); Delsman and Hardenberg (*1*, for young of *H. nehereus*, food habits, and general account); Hora as well as Whitley (*5*; *7*; for *H. translucens*, Australia).

[2] Grey (*2*) has provided a resumé of the deep-water captures of each species.

Characters. Those of the family.

Species. The four named species are *B. ferox* Günther 1878, *B. mollis* Günther 1878 (*3*; *4*: 183, pl. 46, fig. B), *B. agassizi* Goode and Bean 1883, and *B. obtusirostris* Vaillant 1888. *B. obtusirostris* appears to be synonymous with the Pacific *B. mollis*.[3] There are differences between the type descriptions and figures of the North Atlantic *B. agassizi* and the South Pacific *B. ferox*, although every author since (and including) Goode and Bean has considered the two identical. Unfortunately, the type figure of *B. agassizi* is misleading and cannot be reconciled with western North Atlantic specimens. No direct comparison of the Atlantic specimens with those of the western Pacific is possible, as the only Pacific representative is Günther's single type. The North Atlantic *B. agassizi* appears to differ from its Pacific counterpart in the size of the scales and to a lesser degree in morphometric features; it is here retained as a distinct species.

Key to Species

1a. Adipose fin absent; lateral line extending onto caudal fin; base of dorsal fin about as long as distance between nostril and origin of dorsal fin; central pectoral rays branched.

  2a. About 14 scales between origin of anal fin and lateral line, counting obliquely upward and forward. *agassizi* Goode and Bean 1883, below.

  2b. About 8 scales between origin of anal fin and lateral line, counting obliquely upward and forward. *ferox* Günther 1878. Southwestern Pacific.

1b. Adipose fin present; lateral line not extending onto caudal fin; base of dorsal fin much shorter than distance between nostril and origin of dorsal fin, about 1.75 in this distance; central pectoral rays not branched. *mollis* Günther 1878, p. 109.

Bathysaurus agassizi Goode and Bean 1883

Figure 36

Study Material. Four specimens, 181.5–558 mm: one, 540 mm, off the Carolina coast, 647 fms., MCZ 28061, type; 1, 522 mm, ATLANTIS, off New England, 647–1730 fms., MCZ 35101; 1, 558 mm, ALBATROSS, off New England, 40°06′N, 68°01′W, 984 fms., USNM 38106; and 1 small specimen, 181.5 mm, in poor condition, ALBATROSS, off New England, 39°44.5′N, 70°30.75′W, 1081 fms., USNM 43744.

Distinctive Characters. The characters given in the *Key* above will separate this very distinctive fish from all others within the western North Atlantic. It differs from

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[3] *B. obtusirostris* Vaillant (*6*: 136, pl. 10, fig. 2). Vaillant referred this species to *B. mollis* in the explanation of the plates (*6*: 393) of the same work.

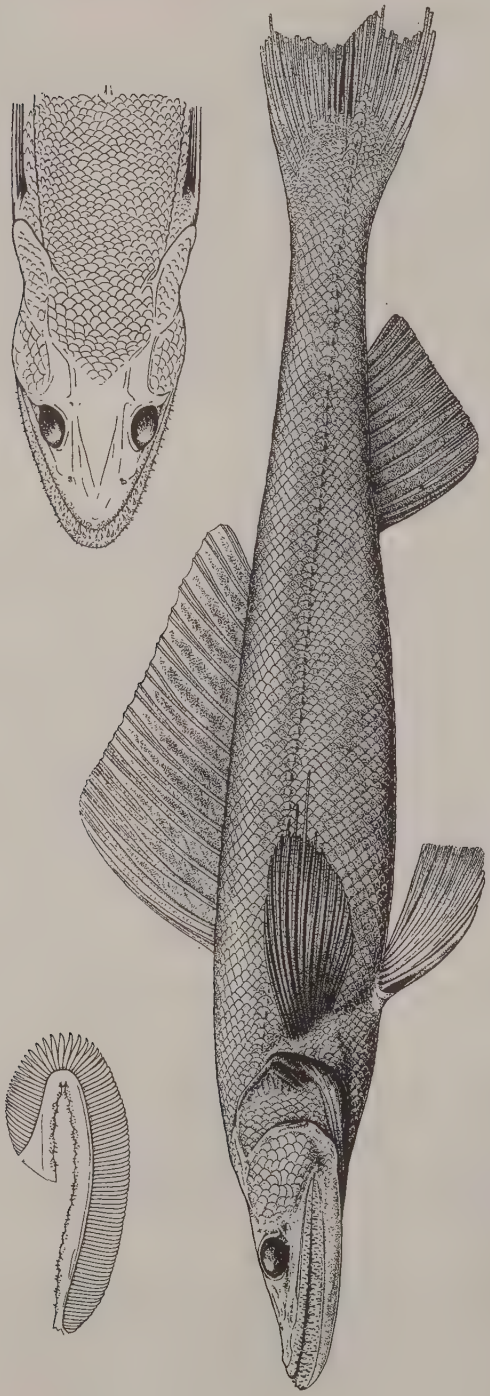

FIGURE 36. *Bathysaurus agassizi*, 522 mm long, from off New England at an undetermined depth greater than 650 fms., MCZ 35101. Drawn by Margaret G. Bradbury.

its congeners by its lack of adipose fin and its smaller and more numerous scales (about 14 between anal origin and lateral line *cf.* 8 in *B. ferox*).[4]

Description. Proportional dimensions in per cent of standard length, based on two adults, 522 and 558 mm long; see *Study Material.*

Body: depth at base of ventral fin 13.6, 16.4; at origin of anal fin 9.4, 9.4; width immediately behind bases of pectoral fins 13.6, 12.5.

Caudal peduncle: least depth 6.2, 5.8.

Head: length 27.6, 27.3; greatest breadth 14.0, 15.2.

Snout: length 8.8, 8.8.

Eye: horizontal diameter 3.6, 3.3; vertical diameter 2.7, 2.2.

Interorbital: width 5.1, 5.1.

Premaxillary: length 18.4, 17.5.

Dorsal fin: length of base 30.6, 31.6; of second ray 14.7, 14.1; of penultimate ray 7.2, 6.5.

Anal fin: length of base 15.0, 14.4; of third ray 9.8, 10.1.

Ventral fin: length 13.5, 15.5.

Pectoral fin: length 25.2, 25.7.

Distance from snout to origin of: dorsal fin 37.2, 34.7; anal fin 72.6, 71.0; ventral fin 34.3, 34.4; pectoral fin 28.0, 29.0.

Scales and Gill rakers: see counts below.

Branchiostegal rays: about 12.

Fin rays: dorsal 17 (first 2 or 3 unbranched); anal 12, 13 (first 2 unbranched); ventral 8; pectoral 15 (upper 2–5 and lower 2 unbranched).

Vertebrae: 63.

BODY deepest just ahead of dorsal fin, this depth 1.7–2.0 in hl; snout and head depressed; trunk almost as broad as deep anteriorly but becoming compressed posteriorly. Least depth of CAUDAL PEDUNCLE 4.4–4.7 in hl (caudal peduncle more slender in juvenile). Vertical fins high and long, partly hidden in median dorsal and ventral grooves when depressed. SCALES present on cheek, opercle, and body, the scales of moderate size, adherent and imbricate; isthmus and branchiostegal membrane naked; no axillary scales; dorsal, anal and paired fins without scales. Rows below lateral line from gill opening to caudal base 79–85, about 13 in the series running obliquely downward and backward from the dorsal origin to the lateral line; about 14 between anal origin and lateral line, counting obliquely upward and forward. About 8 oblique rows on cheek; about 7 on operculum. LATERAL LINE begins at upper angle of gill opening and terminates on lower lobe of caudal fin; about 70 lateral-line scales, five of them on the caudal fin, these scales not corresponding in size or number to adjacent body scales; the central tube pierced above and below by pores.

HEAD depressed and bony, its length 3.6–3.7 in SL, its greatest width, through the cheek, 1.8–2.0 in hl; the lower jaw terminal. SNOUT 3.1 in hl, triangular in dorsal aspect. EYE, PUPIL and ORBIT horizontally elliptical; orbit irregular; horizontal diameter of eye 5.1–5.2 in length of premaxillary. Nostrils double, situated slightly closer to snout than to orbit; the anterior nostril separated from the posterior one by a flap, the length of which is about twice the diameter of the rear nostril. Interorbital broad and bony, 3.4–3.6 in length of premaxillary. Parietals and Post-temperals exposed, separating scales and skin of cheek from that of nape. Preopercle heavy; Opercle, Subopercle, and Interopercle poorly ossified; the subopercle bordering the lower edge and half of posterior edge of gill flap; interopercle small; opercular flap covered by flesh, skin and scales. Branchiostegal membranes thick, extending posteriorly beyond opercular bones, and separated from isthmus and from each other, the left overlapping the right over the isthmus. About 12 poorly ossified Branchiostegal rays, the anterior ones reduced and difficult to count.

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[4] N. B. Marshall has generously recounted the scales on the type specimen of *B. ferox* and has confirmed the counts given by Günther. Einer Koefoed has kindly recounted the scales on the MICHAEL SARS specimens for me, thereby confirming the identity of the eastern and western North Atlantic specimens and substantiating the difference between these and the Pacific *B. ferox.*

Gill rakers on all four arches reduced to spine-bearing tubercles (Fig. 36), about 5 + 18 on first arch. Each tubercle carries a group of spines or gill teeth; also a few minute teeth (on epibranchial) between these tubercles. When the lower limb of the first arch is viewed from above, these tubercles with their spines form two rows; the outer series of tubercles originates on the outer side of the gill arch near its edge, the inner series arises from the inner side of the arch near its edge on the epibranchial and ceratobranchial but near the middle of the inner surface of the hypobranchial segment of the gill arch. Basibranchial and inferior and superior pharyngeals densely covered with teeth of similar size and shape to the gill teeth. The gill arches continue far forward into the mouth and the gill spines contribute to the fearsome aspect of the mouth, every ossified surface of which bears either teeth or spines.

Mouth large, gape about $^2/_3$ as long as head. Rami of Lower jaw not included within upper. Premaxillary long and slender, its length 1.5–1.6 in hl, and partially covered by the suborbital shelf.

Teeth conical, recurved, and mostly depressible; the larger, especially those of the palatines, with weak barbs at their tips. Jaws completely armed save for a small toothless area at symphysis of lower jaw; most of the jaw teeth outside of the mouth. The lower jaw teeth on the outside of the jaws form a broad band, inside of which are two rows of teeth within the mouth that lie between the premaxillary and palatines when the mouth is closed; the inner of these two rows contains the larger teeth. Premaxillary teeth in a broad band, their distribution somewhat patchy, the inner and the anterior teeth largest, the anterior ones directed forward. Largest teeth on the palatines, in two rows, the teeth of the inner series larger.

Vertical fins high and long, partly hidden in median dorsal and ventral grooves when depressed. Dorsal fin anteriorly placed, its origin over base of ventral fin; the predorsal distance 2.7–2.9 in SL; its base long, 3.2–3.3 in SL. Anal long, its base 6.7–6.9 in fish length, the preanal distance 1.4 in length. Caudal fin but slightly forked (broken in all study specimens), the procurrent rays covered with skin. Paired fins forming horizontal planes when expanded. Ventral fins with truncate edge. Central Pectoral ray or rays elongate.

Anus and genital openings immediately ahead of anal origin.

Color. In preserved specimens, body brown, darker below than dorsally. Scale pockets lined with black. Vertical fins darker than body; paired fins nearly black. Branchiostegal membrane and linings of mouth and of pharyngeal and abdominal cavities black.

Synonyms and References:

Bathysaurus agassizii Goode and Bean, Bull. Mus. comp. Zool. Harvard, *10* (5), 1883: 215 (orig. descr., Albatross St. 325, 33°35′20″N, 76°W, 647 fms., MCZ 28061); Günther, Rep. sci. Res. 'Challenger', Zool., *22*, 1887: 183 (refers *B. agassizi* to *ferox*); Vaillant, Exped. Sci. 'Travailleur' 'Talisman', Poiss., 1888: 139, pl. 10, fig. 1 (descr. 455-mm spec. from St. 39; 2200 m off Morocco); Agassiz, Bull. Mus. comp. Zool. Harvard, *15* (Three Cruises of the 'Blake') 2, 1888: 32, fig. 216 (no descr. or loc.); Garman, Mem. Mus. comp. Zool. Harvard, *24*, 1899: 400 (listed, from Goode and Bean, 1895 and Vaillant, 1888); Jordan, Evermann and Clark, Rep. U.S. Comm. Fish. (1928), App. 10, 1930: 164 (listed); Grey, Fieldiana: Zool., *36* (2), 1956: 128 (in part; distr.).

Bathysaurus ferox (*non* Günther), Vaillant, Exped. Sci. 'Travailleur' 'Talisman', Poiss., 1888: 393 (refers his fish, descr. under name *B. agassizi*, to *B. ferox* on Günther's auth.); Goode and Bean, Smithson. Contrib. Knowl., *30*, 1895: 58, pl. 18, figs. 65–66 (descr., Albatross St. 2710, 984 fms.; St. 2051, 1106 fms.; St. 2550, 1081 fms.; St. 2104, 991 fms.; erroneously refers *B. obtusirostris* to *ferox* in appendix, p. 510); Jordan and Evermann, Bull. U.S. nat. Mus., *47* (1), 1896: 539 (descr., from Goode and Bean, 1895); Jordan and Evermann, Rep. U.S. Comm. Fish. (1895), App. 5, 1896: 297 (listed); Murray and Hjort, Depths of Ocean, 1912: 120, fig. 103; and elsewhere (recs. of Michael Sars spec.; see Koefoed, 1927); Koefoed, Rep. 'Michael Sars' N. Atlantic Deep-Sea Exped., *4* (1), 1927: 62, pl. 4, fig. 4 (descr. e. N. Atl. spec. from Michael Sars St. 25, 35°46′N, 8°16′W, 2055 m; St. 35, 27°27′N, 14°52′W, 2603 m; St. 53, 34°59′N, 33°01′W, 2615 m; St. 88, 45°26′N, 25°45′W, 3120 m; St. 95, 50°22′N, 11°44′W, 1797 m, *cf. B. mollis*); L. L. Rey, Mem. Acad. Cien., Ser. Cien. Nat., *11*, 1947: 382, pl. 6, fig. 3 (from Günther, 1887, and Murray and Hjort, 1912, descr.); Schroeder, Copeia, 1940: 233 (rec. of spec., MCZ 35101; see *Study Material*, p. 105); Hubbs, J. Morph., *33* (1), 1919: 64 (branchiostegal rays); Dollfus, Trav. Inst. sci. Chérifien, (Zool.) 6, 1955: 37 (listed, from lit.).

Doubtful References[5]:

Bathysaurus ferox, Barnard, Ann. S. African Mus., *21* (1), 1925: 228 (descr.; off Table Bay, S. Africa, 600–1400 fms.); Gilchrist and von Bonde, Rep. Fish. Mar. Biol. Surv. Union S. Africa (1928), *3* (7), 1924: 12 (rec. from Pickle St. 354, 626 fms.; St. 517, 600 fms.; St. 526, 1400 fms.); Fowler, Bull. Amer. Mus. nat. Hist., *70* (1), 1936: 345 (descr. and fig. from Günther, 1887); Smith, J. L. B., Sea Fishes S. Africa (1949), 1950: 113, fig. 179 (diagn.).

Bathysaurus mollis Günther 1878

Figure 37

Study Material. Two juvenile specimens from the Gulf of Mexico, in the USNM and MCZ: 1, 215.5 mm SL, Oregon St. 2567, 24°41′N, 91°02′W, 1750–1725 fms., a bottom-trawl haul, July 25, 1959; 1, 188.5 mm, Oregon St. 2577, 27°48′N, 88°45′W, 850–1100 fms., otter trawl, July 30, 1959.

Distinctive Characters. The characters given in the *Key* (p. 105) will separate this species from all others in the western North Atlantic.

Description. Proportional dimensions in per cent of standard length, based on the two juvenile study specimens, 215.5 and 188.5 mm SL.

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[5] I have seen no South Atlantic specimens, and the accounts referred to do not include the character that I have used to distinguish *B. agassizi* from *B. ferox*.

Body: depth at base of ventral fin 8.5, 10.8; at origin of anal fin 7.6, 8.3; width immediately behind bases of pectoral fins 9.4, 9.0.

Caudal peduncle: least depth 5.0, 5.4.

Head: length 22.3, 23.9; greatest breadth 11.8, 12.2.

Snout: length 5.8, 6.2.

Eye: horizontal diameter 4.0, 3.8; vertical diameter 3.1, 3.2.

Interorbital: width 4.3, 4.5.

Premaxillary: length 16.6, 16.8.

Dorsal fin: length of base 16.5, 19.4; of third ray 17.6, —; of penultimate ray 7.5, 8.4.

Anal fin: length of base 13.7, 14.3; of third ray 10.8, 11.6.

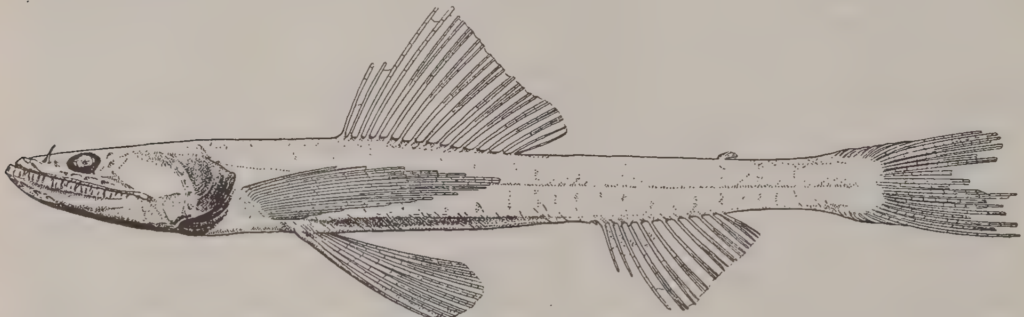

Figure 37. *Bathysaurus mollis*, 188.5 mm long, from the central Gulf of Mexico, Oregon St. 2577, 27°48′N, 88°45′W, 850–1100 fms. Drawn by Margaret G. Bradbury.

Ventral fin: length 19.7, 19.5.

Pectoral fin: length 25.1, 30.0.

Distance from snout to origin of: dorsal fin 36.6, 37.6; anal fin 69.1, 68.2; ventral fin 32.9, 33.8; pectoral fin 24.6, 25.9.

Branchiostegal rays: 8.

Fin rays: dorsal 16–17 (first 4 unbranched); anal 13 (first 4 unbranched); ventral 8; pectoral 16 or 17.

Vertebrae: 50 or 51.

Body deepest just ahead of dorsal fin, this depth 2.2–2.6 in hl; snout and head depressed; trunk almost as broad as deep anteriorly but becoming compressed posteriorly. Least depth of Caudal peduncle 4.4–4.5 in hl. Vertical fins high; not hidden in grooves when depressed as in *B. ferox* adults. Scales present on cheek, opercle and body, the scales of moderate size, imbricate and decidous (all lost in both study specimens).

Head bony, its length 4.2–4.5 in SL, its greatest width, through the cheek, 1.9–2.0 in hl; the lower jaw terminal. Snout 3.8 in hl, rounded (*cf.* triangular in *B. ferox*). Eye, Pupil, and Orbit horizontally elliptical; orbit asymmetrical; horizontal diameter of eye 4.2–4.5 in length of premaxillary. Nostrils located slightly closer to orbit than to snout, the membrane between the anterior and the posterior nostril developed into a cirrus of about the same length as the pupil. Interorbital broad and bony, 3.7–3.9 in length of premaxillary. Preopercle heavy; Opercle, Subopercle and Inter-

OPERCLE poorly ossified; subopercle bordering lower edge and half of posterior edge of gill flaps; interopercle small. BRANCHIOSTEGAL MEMBRANES extending beyond head, heavy and muscular anteriorly, becoming membraneous posteriorly, separated from one another and from the isthmus anteriorly, the left slightly overlapping the right. BRANCHIOSTEGAL RAYS about 8; the anterior ones weak and poorly ossified.

GILL RAKERS present on all four arches but reduced to spinulose plates, about 6 + 15 groups of spines on first arch; in form and arrangement similar to those of *B. ferox* (p. 106).

MOUTH large, the gape about $^2/_3$ as long as head. Rami of LOWER JAW not included within the upper. PREMAXILLARY long and slender, not notably expanded posteriorly, partly covered by suborbital shelf; its length 1.3 or 1.4 in hl.

TEETH recurved and mostly depressible, the larger ones barbed. Jaws completely armed except for a small toothless area at symphysis of lower jaw; most jaw teeth outside of mouth. The arrangement and size of all teeth similar to *B. ferox* (p. 108).

Vertical fins high; the dorsal and anal, when depressed, not hidden in grooves in the body as in *B. ferox*. DORSAL fin originating well behind insertion of ventral fin, the predorsal distance about 2.7 in SL, the length of its base about 1.2 in hl. ADIPOSE fin narrow and high, over posterior end of base of anal. ANAL fin originating far behind end of base of dorsal, the preanal distance 1.4–1.5 in SL, the length of its base 1.6 or 1.7 in hl. Paired fins forming horizontal planes when expanded. VENTRAL fins with truncated rear edge. Central PECTORAL rays elongate.

Anal and genital openings immediately anterior to origin of anal fin.

Color. In preserved specimens, body white, these specimens retaining the juvenile series of about 16 narrow and faint vertical crossbars; in the interspaces between them, a shorter bar not extending upward beyond the lateral line. Peritoneal, pharyngeal, buccal, and opercular linings black. Dorsal fin colorless; anal, caudal, and paired fins dusky.

Prior to preservation, body colorless save for the linings of the body cavities and eyes. The top of the head was transparent and the brain easily seen from above. Pupil and lens light green.

Size. Although *B. mollis* is known from the western North Atlantic only from the two juveniles described above, the species elsewhere attains a length of at least 19 inches.

The species is benthonic; nothing is known about its development or life history.

Range. B. mollis is now known from the eastern North Atlantic at depths of 2615–4360 m; the Gulf of Mexico at 3150–4700 m; the Pacific off Lower California at 3220 m; the South Pacific at 4361 m; and the western Pacific off Japan at 3429 m.

Synonyms and References:

Bathysaurus mollis Günther, Ann. Mag. nat. Hist., (5) *2*, 1878: 182 (orig. descr.; middle of S. Pac.; off Yedo; 1875 and 2385 fms., CHALLENGER); Günther, Rep. sci. Res. 'Challenger', *22*, 1887: 183, pl. 46B (descr. CHALLENGER spec.); Vaillant, Exped. Sci. 'Travailleur' 'Talisman', Poiss., 1888: 439 (comp. *B. mollis* and *B. obtusirostris* Vaillant); Goode and Bean, Smithson. Contrib. Knowl., *30*, 1895: 59 (orig. Günther account mentioned); Garman, Mem. Mus. comp. Zool. Harvard, *24*, 1899: 400 (listed from Günther, 1878 and 1887); Murray and Hjort, Depths of Ocean, 1912: 414 (Günther CHALLENGER and Vaillant's (*B. obtusirostris*) TALISMAN locs. listed); Vaillant *in* Roule, Résult. Camp. Sci. Monaco, *52*, 1919: 130 (spec. from St. 753; 39°50′N, 17°58′W, 4360 m); Townsend and Nichols, Bull. Amer. Mus. nat. Hist., *52* (1), 1925: 10, pl. 1:1 (ALBATROSS St. 5684, Pac. off Lower California near 23°N, 1760 fms.); Koefoed, Rep. 'Michael Sars' N. Atlantic Deep-Sea Exped., *4* (1), 1927: 62 (descr. spec. from St. 53, 34°59′N, 33°01′W, 2615 m); Fowler, Bull. Amer. Mus. nat. Hist., *70* (1), 1936: 346, fig. 1 (synonymy and descr., fig. from Günther's 'Challenger' Rep., 1887); Grey, Fieldiana: Zool., *36*, 1956: 129 (detailed synopsis of distr. from lit.); Nybelin, Rep. Swedish Deep-Sea Exped., *2* (Zool.) 20, 1957: 252 (one spec. from Swedish ALBATROSS St. 313 (haul 1): 29°48′N, 17°39′W to 30°05′N, 17°18′W, June 16, 1948, 4267–4255 m).

Bathysaurus obtusirostris Vaillant, Exped. Sci. 'Travailleur' 'Talisman', Poiss., 1888: 439, pl. 10:2 and 14:3 (orig. descr., one spec. from 3655 m off Cape Verde Is.); Garman, Mem. Mus. comp. Zool. Harvard, *24*, 1899: 400 (listed, from Vaillant, 1888).

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Family Chlorophthalmidae

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Reprinted from Memoir Sears Foundation for Marine Research, I (5), 1966: 162–189.

Family Chlorophthalmidae

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Characters.[2] MODERATELY SLENDER BOTTOM FISHES OF THE CONTINENTAL SHELF AND DEEP SEA WHICH, AS ADULTS, ARE NORMALLY UNDER 12 INCHES LONG. Body compressed posteriorly, nearly round in cross section anteriorly; the ventral surface somewhat flattened. Eyes large and directed dorsolaterally, entering into dorsal profile; round or horizontally elliptical. Pupil keyhole-shaped, the lensless aphakic space anterior to the lens conspicuous. Tapetum of eye an iridescent green in life. Interorbital space narrow or moderately narrow, flat or slightly concave. Supraorbital bone free from skull or completely absent.

Scales present on cheeks, opercles, body, and base of caudal fin, those on side of head usually lost during capture; top of head naked; scales on cheek of about the same size as those on body, which are ctenoid or cycloid. Lateral line complete, not extending onto caudal fin, but terminating at base of midcaudal ray.

Dorsal fin in anterior half of body, its base shorter than the combined lengths of snout and eye, and formed of about 9–13 rays. Base of anal fin shorter than that of dorsal, the fin originating in the posterior half of the body and containing 7–11 rays. Caudal fin forked, the lobes approximately equal in length, the fin composed of 19 (1-17-1) principal rays. Ventral fins inserted approximately under origin of dorsal fin and in the middle third of the length of the fish; the fins lying in an oblique plane when expanded; composed of 8 or 9 rays, the tips of the rays not thickened. Pectoral fins entire and without prolonged rays, their insertion below the middle of the side of the body, and formed of 15–17 rays. Adipose fin well developed, located over base of anal fin.

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[1] This study was completed while the author was with the Ichthyological Laboratory, U.S. Fish and Wildlife Service, U.S. National Museum.

[2] Based chiefly on specimens and descriptions of the species of *Chlorophthalmus* and *Parasudis*. Since I have but one representative of the three named species of *Bathysauropsis* I have not been able to include this genus in the family characterization. No species of *Bathysauropsis* from the North Atlantic is known, and the three species seem to differ markedly from one another. The one available specimen, the holotype of *B. malayanus* (Fowler), has the following features that are at variance with the characterization of the family provided above: tongue, although free at its tip, much smaller than in *Parasudis* and *Chlorophthalmus*; gill arches extending farther forward into the large mouth, farther than the angle of the gape; 22 or 23 pectoral fin rays; anus situated in posterior third of distance between origin of ventral fin and origin of anal; and most palatine teeth larger than those in jaws. A critical study of *Bathysauropsis* may show that it should be placed in a family distinct from, although related to, the Chlorophthalmidae.

Anus located in anterior two-thirds of distance between insertion of ventral fin and origin of anal fin; a minute anal papilla present.

No luminous organs.

Lower jaw terminal. Suspensorium anteriorly inclined. Upper jaw extending posteriorly to below anterior edge of orbit in some, to below eye in others, and to below rear edge of orbit in a few. Both maxillary and premaxillary well developed, the maxillary dilated behind and with a single supramaxillary bone.

Tip of tongue free and well developed, supported by a horizontal glossohyal bone.

Teeth on jaws, vomer, and palatines; none on tongue; teeth small and needle-shaped, slightly recurved, sometimes slightly barbed at the tip, and mostly depressible. Aside from the pair of stronger needle-like teeth on the vomer of *Parasudis* and the palatine teeth of *Bathysauropsis*, none is enlarged or lanceolate.

Gill arches extending no farther forward into mouth than the angle of the gape (except in *Bathysauropsis*). Gill rakers of the usual lath-like shape, longer or shorter than the gill filaments opposite to them. Pseudobranchiae well developed, located high in gill cavity and partly covered by a fold of black skin. Branchiostegal membrane not extending posteriorly beyond opercular flap. Branchiostegal rays about eight, four inserted on the epihyal and four on the ceratohyal. Gill membranes joined to one another across isthmus anteriorly by a broad but thin fold. Opercular flap thin, its posterior margin formed by both the opercle and the subopercle. Interopercular bone not reduced.

All the species that have been studied are monoecious.

Vertebrae (western Atlantic *Chlorophthalmus* and *Parasudis*), 38–49.

Remarks. All the chlorophthalmids are benthonic. One genus, *Bathysauropsis*, occurs in very deep water (p. 186). The other two, *Parasudis* and *Chlorophthalmus*, contain species that are common in the North Atlantic at depths between 100 and about 400 fathoms. The common Australian species, *C. nigripinnis*, lives in more shallow water and is common at depths between 25 and 70 fathoms (7). These fishes are abundant but of no direct use to man. The adults are normally between six and twelve inches long.

Genera. Three genera are here recognized: *Chlorophthalmus*, *Parasudis*, and *Bathysauropsis*.

Key to Genera

1a. Anus closer to base of ventral fin than to base of anal fin; maxillary terminating anterior to a vertical from center of eye; origin of dorsal fin anterior to origin of ventral fin.

2a. Horizontal diameter of eye less than 1.25 in snout; anus close to bases of inner ventral rays, separated from these bases by 2 or 3 scales; palatine teeth minute and restricted to anterior half of bone; no one of the vomerine teeth notably larger than the rest. *Chlorophthalmus* Bonaparte 1840, below.

2b. Horizontal diameter of eye more than 1.25 in snout; anus well behind bases of inner ventral rays, separated from them by 8–10 rows of scales; a broad band of strong palatine teeth; each side of vomer with a single strong fixed and enlarged fang set in a heavy bony socket. *Parasudis* Regan 1911, p. 179.

1b. Anus closer to base of anal fin than to base of ventral fin; maxillary extending beyond posterior edge of eye; origin of dorsal fin posterior to origin of ventral fin. *Bathysauropsis* Regan 1911, p. 185.

Genus *Chlorophthalmus* Bonaparte 1840

Shortnose Greeneye

Chlorophthalmus Bonaparte, Icon. Fauna Ital., *3*, 1840; type species, by monotypy, *C. agassizi* Bonaparte 1840; Mediterranean.

Generic Synonyms:

Hyphalonedrus Goode, Proc. U.S. nat. Mus., *3*, 1881: 483; type species, by monotypy, *H. chalybeius* Goode 1881: 484; south of Nantucket, Massachusetts, 120–142 fathoms.

Pelopsia Facciolà, Nat. Sicil., *2*, 1882–83: 145; type species, designated by Jordan, Stanford Univ. Publ., Univ. Ser., Biol. Sci., *4*, 1920: 423; *P. candida* Facciolà, 1882–83; Mediterranean.

Characters. Snout short, broad and depressed, its length usually less than the horizontal diameter of the eye. Maxillary excluded from gape and ending under anterior half of orbit. Head usually broader than deep. Body nearly round in cross section anteriorly, compressed posteriorly. Gill flap extending to upper end of pectoral base or beyond (in Atlantic species). Dorsal fin originating in advance of ventral fin. Inner ray of ventral fins black. Anus usually black, separated from bases of inner rays of ventral fins by 2 or 3 rows of scales, located in the first third of the distance between base of outer ventral ray and origin of anal fin. Teeth small, mostly depressible. No enlarged fixed fangs on vomer or palatines. Teeth on each side of vomer in a row or a patch, these patches usually continuous with each other through a single row of smaller teeth along the anterior edge of the vomer. Palatine teeth small and restricted to anterior half of that bone. Tongue and basihyal broad. Gill rakers moderately long and slender, more than 14 on lower limb of first arch.

Habits. Little is known of the habits of the species of *Chlorophthalmus* other than from the reports of Sanzo and of Tåning on the planktonic young of *C. agassizi* (p. 174). The adults of these fishes are thought to be bottom residents.

Range. The species of this genus occur at moderate depths throughout the tropical and temperate regions of the world.

Species. Seventeen named species of *Chlorophthalmus* are usually recognized: *C. agassizi* Bonaparte (*4*), type locality, Mediterranean; *C. nigripinnis* Günther (*13*; *14*: 133, pl. 6, fig. 5), Twofold Bay, Australia, 120 fms.; *C. chalybeius* (Goode) (*11*), off Nantucket, Massachusetts, 120 fms.; *C. productus* Günther (*14*: 193, pl. 50, fig. D), Fiji Islands, 315 fms.; *C. corniger* Alcock (*1*, *2*, *3*), Bay of Bengal, 145–250 fms.; *C. proridens* Gilbert and Cramer (*9*), Hawaii, 295–310 fms.; *C. mento* Garman (*8*), Pacific coast off Panama, 210–286 fms.; *C. albatrossis* Jordan and Starks (*16*), Suruga and Sagami Bays, Japan; *C. punctatus* Gilchrist (*10*), South Africa, 154 fms.; *C. bicornis* Norman (*23*), Gulf of Aden, 274–366 m; *C. acutifrons* Hiyama (*15*), Kumano-nada, Japan, 500 m; *C. borealis* Kuronuma and Yamaguchi (*20*), Chosi Fish Market, Japan; *C. atlanticus* Poll (*27*), tropical West Africa, 75–450 m; *C. oblongus* Kamohara (*18*: 2, fig. 1), Mimase fish market, Japan; *C. acutifrons nigromarginatus* Kamohara (*18*: 5), Mimase market, Japan; *C. japonicus* Kamohara (*19*), off Okitsu, Prov. Tosa, Japan; and *C. brasiliensis* Mead (*21*), off northeastern Brazil, 125–275 fms.

A comparison of specimens from a large number of western North Atlantic localities has shown that the commonest species, *C. agassizi*, is highly variable and that more material is necessary for the proper definition of subspecies and geographical or ecological races. The second species, *C. brasiliensis*, is known only from a small area off Brazil. No attempt has been made to review the entire family on the basis of published accounts and the few specimens available, these being from widely separated localities. There are, however, groups of species that differ from other groups, and a note on these is in order.

The circumglobal complex of highly variable species or subspecies, of which *C. agassizi* is the earliest described representative, contains the following nominal forms: *agassizi*, *productus*, *proridens*, *atlanticus*, *chalybeius*, *brasiliensis*, *albatrossis* and *borealis*. The last two of these were considered subspecies of *albatrossis* by Kamohara (*18*: 1; *19*). Parr (*24*) excluded *agassizi* from this group (the "*nigripinnis*" group of Parr) on the basis of relative head length and number of scales. The variability shown by the Atlantic material makes this dichotomy subject to question. His exclusion of *chalybeius* was based on an error, for the maxillary of the type of *chalybeius* extends to beneath the anterior margin of the pupil, as stated in the type account, and not "to the vertical from the anterior margin of the orbit" (*24*). Although *chalybeius* may represent a northern form of *agassizi*, there is not enough material available at present to warrant such a separation. The two Japanese subspecies of *C. albatrossis*, *C. a. albatrossis* and *C. a. borealis* (of Kamohara) are also very closely allied to *C. agassizi*. I concur with Parr's union of Günther's *productus* with *agassizi*, and I also include the African *atlanticus* within the synonymy of that species. Although some of these may be distinct, the evidence for specific separation is slight in the light of the geographical variability that is known to occur. *C. brasiliensis* is discussed on p. 176.

I have not seen specimens of the Japanese *C. oblongus*, but the type account portrays a fish that can easily be separated from its congeners because it has only a few (2.5) rows of scales between the lateral line and the base of the dorsal fin. *C. japonicus* appears to be closely related to it.

The Pacific Panamanian *C. mento* is probably distinct, for in addition to differences in dentition and body form, its ventral fins are inserted farther forward than those of other species of *Chlorophthalmus*.

C. corniger, *C. acutifrons acutifrons* and *C. a. nigromarginatus* are the most highly specialized of the species of *Chlorophthalmus*. They have longer and more depressed snouts, stronger vomerine teeth, shorter and fewer gill rakers, and a more posteriorly situated anus than any other species of *Chlorophthalmus*, being intermediate in these respects between the more conservative species of *Chlorophthalmus* and *Parasudis truculentus*. I have examined a series of *C. corniger* from the Philippine Islands and have noted a relative change in the snout-to-eye ratio with growth. Other differences in body proportion with growth are also apparent, and while Alcock's type of *corniger* was small, those of the Japanese *C. a. acutifrons* and *C. a. nigromarginatus* are large. The *corniger-acutifrons* group requires a study based on material from throughout the western Pacific and Indian oceans.

Key to Western North Atlantic Species

1a. Length of snout more than 1.3 in horizontal diameter of orbit,[3] more than 1.6 in width of head immediately behind orbit; distance from tip of upper jaw to tip of lower (mouth closed) more than 7 in width of head measured just behind orbit.
agassizi Bonaparte 1840, below.

1b. Length of snout less than 1.3 in horizontal diameter of orbit, less than 1.6 in width of head immediately behind orbit; distance from tip of upper jaw to tip of lower (mouth closed) less than 7 in width of head measured just behind orbit.
brasiliensis Mead 1959, p. 176.

Chlorophthalmus agassizi Bonaparte 1840

Shortnose Greeneye

Figures 44, 45

Study Material. More than a thousand western North Atlantic specimens, 40–125.5 mm SL, in USNM, MCZ, CNHM, UMML, TU, BLBG, and UF. The localities at which these collections were made are indicated on Fig. 44.[4]

The extralimital material examined included specimens of *C. agassizi* from the Mediterranean; *C. corniger* and *C. proridens* (types); *C. mento* (including types); *C. alba-*

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[3] Because of the relatively small size of the eye in specimens of *C. agassizi* from the northern part of its range (New England, "*chalybeius*-type"), the snout-in-eye ratio in that population approximates 1.3. No trouble should arise when examining specimens from farther south.

[4] Almost all specimens were collected by bottom trawl or dredge by the U.S. Bureau of Fisheries and Fish and Wildlife Service vessels FISH HAWK, BLAKE, ALBATROSS I, ALBATROSS II, ALBATROSS III, PELICAN II, OREGON and COMBAT; the Woods Hole Oceanographic Institution vessels ATLANTIS, CARYN and CAP'N BILL II (chartered); and by the yacht CAROLINE (Smithsonian Institution Expedition).

trossis (types) and *C. atlanticus* (paratypes, loaned by Dr. Max Poll, Curator of Vertebrates, Musée Royal du Congo Belge, Tervuren, Belgium).

Distinctive Characters. The general form of the snout and eye and the more robust form of the body distinguish *C. agassizi* from the only other western North Atlantic species, *C. brasiliensis*. Characters included in the *Key to Species* (p. 166) and in the diagnosis of *C. brasiliensis* (p. 176) will separate the two species. The attributes of the infraspecific populations of *C. agassizi* are discussed on p. 172.

Description. A total of 189 specimens, 45–152 mm SL, representing all western Atlantic continental shelf areas, were used to obtain the range of measurements for the characters showing the greatest variability: length of head and premaxillary, width of head, horizontal diameter of orbit, width of interorbital, width of body at insertion of pectoral fin, and least depth of caudal peduncle. The measurements for the other characters are from 30 specimens, 74.5–137 mm SL, representing two populations that differ greatly from each other (a sample from the western Gulf of Mexico and another from off South Carolina). Proportional dimensions in per cent of standard length.

Body: depth at origin of dorsal fin 12.6–18.8; depth at origin of anal fin 9.6–11.7; width at insertion of pectoral fins 12.2–15.6.

Caudal peduncle: least depth 6.0–8.2.

Head: length 27.0–33.5; width between most anterior points of orbit 8.7–12.6; width between most posterior points of orbit 12.1–17.1.

Snout: length from tip of upper jaw to nearest point of eye 8.4–10.0; to end of maxillary 10.8–14.9.

Eye: horizontal diameter 10.2–13.2; vertical diameter 8.0–11.4.

Orbit: horizontal diameter 9.5–14.5; vertical diameter 8.5–11.4.

Bony interorbital: width 1.6–2.5.

Dorsal fin: length from origin to tip, depressed 21.0–23.7.

Anal fin: length 13.8–16.0.

Pectoral fin: length 25.0–28.5.

Scales in lateral series: 50–55 between upper point of gill opening and base of midcaudal ray.

Gill rakers: on lower limb of anterior arch 19–22.

Fin rays: dorsal 10 or 11; anal 7–9; caudal 1-17-1; ventral 8 or 9; pectoral 15–17.

Vertebrae: 46 + 1.[5]

Because of the great geographical variability in the characters of *C. agassizi*, several of the head and body measurements expressed as fractions of other measurements are meaningless if data from all areas of distribution are combined. The tabulations in Table 1 for different areas are considered more useful.

BODY compressed posteriorly but nearly circular in cross section anteriorly, its greatest depth under dorsal fin, its depth at origin of anal fin 2.3–3.3 in hl (in adults over 100 mm long), the width at insertion of pectoral fin 1.8–2.4 in hl.

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[5] Vertebrae 46–48, with a mean of 46.8; from X-ray photographs of 155 specimens from the Gulf of Mexico and Atlantic coast from Florida to New England. There is no significant correlation between vertebral number and latitude.

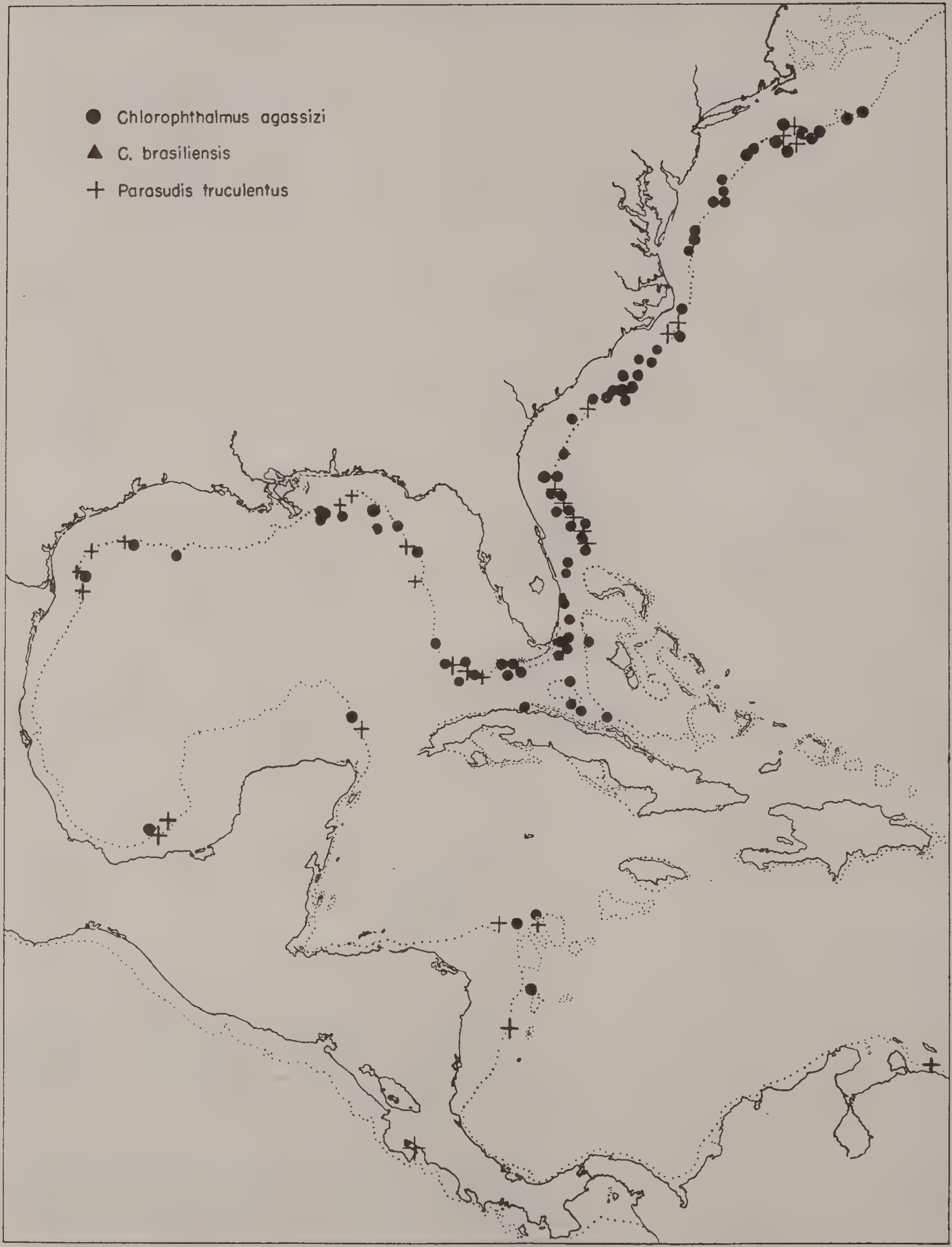
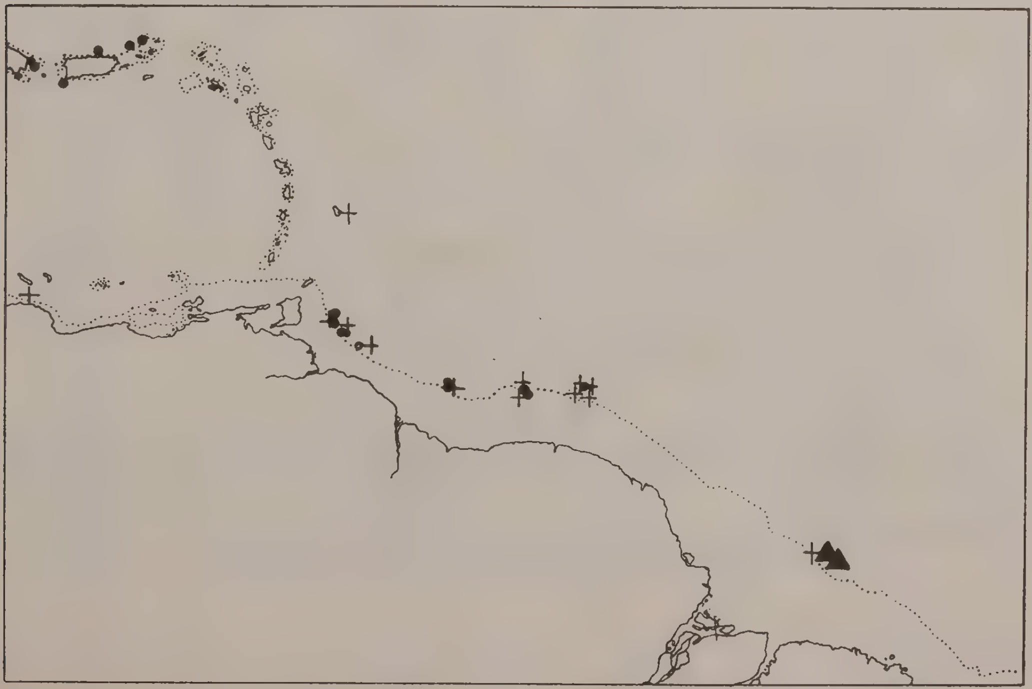

● Chlorophthalmus agassizi
▲ C. brasiliensis
+ Parasudis truculentus

FIGURE 44. *Opposite* and *above*: the distribution, in the western North Atlantic, of *Chlorophthalmus agassizi*, *C. brasiliensis*, and *Parasudis truculentus*.

Table I. Ranges of Certain Ratios of Body Parts in *C. agassizi* for Different Geographical Areas of its Distribution

Locality	Premaxillary length into hl	Greatest preorbital width of head into hl	Width of head between posterior midpoints of orbit into hl	Horizontal diameter of orbit into hl	Width of bony interorbital into hl	Width of bony interorbital into horizontal diameter of orbit	Least depth of caudal peduncle into hl
Atlantic coast							
N. of 35°N	2.30–2.46	2.64–3.03	1.97–2.19	2.63–3.08	12.8–15.4	4.64–5.75	3.25–3.78
From 35°N to southern tip of Florida	2.22–2.43	2.48–2.82	1.93–2.13	2.41–2.69	13.8–16.4	5.36–6.80	3.61–4.50
Gulf of Mexico							
Northeastern section	2.17–2.42	2.54–2.76	1.88–2.10	2.21–2.59	13.6–19.9	6.08–8.25	3.57–4.63
Northwestern section	2.20–2.44	2.43–2.94	1.87–2.06	2.27–2.40	14.5–18.6	6.18–7.70	4.30–5.22
Western Campeche Bank	2.24–2.34	2.62–2.99	1.86–2.02	2.32–2.43	15.0–16.6	6.20–7.14	4.68–5.12
Eastern Campeche Bank	2.20–2.39	2.45–2.75	1.82–2.06	2.32–2.54	13.7–17.8	5.22–6.80	3.74–4.59
Caribbean and northern S. America							
Barbados	2.25–3.07	2.52–2.96	1.86–2.07	2.29–2.68	13.3–18.5	5.51–7.95	3.99–5.29
Venezuela and the Guianas	2.22–2.46	2.56–2.77	1.84–2.06	2.25–2.45	13.3–15.3	5.33–6.38	4.18–4.78

Scales covering body, suborbital region of head, and caudal base; snout, interocular and opercular surfaces, and jaws scaleless. The scales imbricate, weakly denticulated, cycloid, and deciduous. No prominent axillary scales; those in axil of pectoral and ventral fins slightly stronger and larger than adjacent body scales, and with smooth



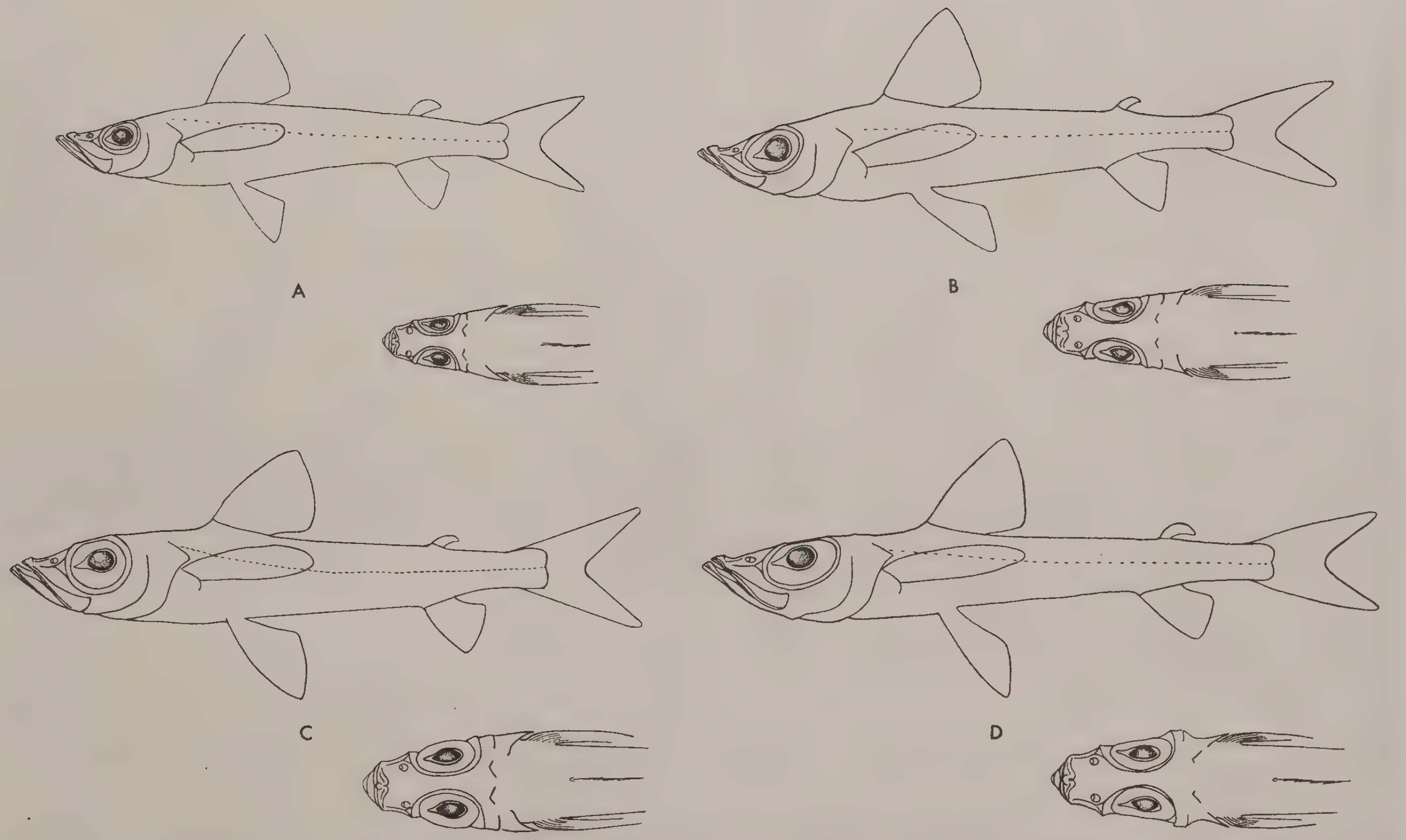


Figure 45. *Chlorophthalmus agassizi.* Four specimens, each about 120 mm long, representing four of the geographical variants: a, a specimen from off Nantucket Island; b, from off South Carolina; c, from the eastern Campeche Bank adjacent to the Yucatán Channel; and d, the western Campeche Bank, 19°37′N, 92°40′W. Drawn by Mildred H. Carrington.

edges. About five rows of smaller scales overlying the bases of the caudal rays. An enlarged median scale covering the bases of the inner ventral fin rays. LATERAL-LINE scales with pores and with stronger denticulations than those on most body scales.

HEAD broad; SNOUT depressed; LOWER JAW terminal. EYE large and horizontally elliptical (more nearly circular in Atlantic populations than in the Gulf of Mexico, especially the western Gulf, forms); eyes directed dorsolaterally, those of larger individuals directed more strongly upward than those of smaller specimens. INTERORBITAL space narrow. The most posterior point of orbit produced laterally into blunt bony points which are more prominent in the western Gulf of Mexico and South American forms than in the others. Posterior part of head terminating in a flap extending beyond the base of upper pectoral fin rays. Head covered by an extensive network of SENSORY PORES and channels which are difficult to describe satisfactorily because of the loss of skin from almost all specimens. This system is most highly developed on the interorbital region (a central channel with transverse tubes extending onto the dorsal dermal eyelid), on the circumorbital system, and on the ventral surface of the head.

GILL RAKERS long and flattened on the anterior two arches but reduced to spine-bearing knobs on the succeeding two; rakers on lower limb of first arch slightly longer than the opposing gill filaments; each bearing minute spines along its inner edge.

Angle of gape under, or just before, anterior edge of orbit. PREMAXILLARY extending to a vertical from anterior edge of pupil in New England specimens, or slightly beyond this point in more southern representatives. LOWER JAW extending beyond the upper, its tip formed of a well-ossified bony plate variously sculptured and adorned with bony protuberances and teeth;[6] the lower terminal part of this jaw tip formed of three bony protuberances, which form a slightly concave triangle; the profile of tip of mandible, as viewed from above, evenly rounded or concave depending on the size of the individual and the locality from which it came.

TEETH present on mandible, premaxillary, vomer, and palatine bones; minute tooth-like denticles on tongue. Premaxillary teeth in a narrow band; minute and approximately equal in size; the inner ones slightly recurved; all depressible. A row or patch of teeth on each lateral knob of vomer; these usually continuous with one another through a single row of smaller teeth along anterior edge of vomer; some fixed; others depressible. Palatines with a few very small and easily overlooked teeth anteriorly. Behind the plate at tip of lower jaw is a median toothless knob flanked by irregular patches of depressible recurved teeth which are not included within the upper jaw when mouth is closed; a band of mandibular teeth originating on either side of symphyseal ridge, this band broader and the teeth larger anteriorly than laterally; teeth becoming sparse posteriorly. All or almost all mandibular teeth depressible.

DORSAL fin inserted in advance of origin of ventral fin, the 2nd, 3rd or 4th ray longest, the 3 frequently of almost equal length. Height of dorsal fin from origin to tip when depressed, 4.3–4.9 in SL. ADIPOSE fin situated over, or slightly in advance of, middle of base of anal fin; its height about two-thirds of horizontal diameter of eye. Depressed height of ANAL fin 6.3–7.5 in SL.

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[6] This plate has been considered of some taxonomic value, but I fail to find any feature of it consistent enough to permit its use as a reliable character for the separation of western North Atlantic populations.

Color. In alcohol, background color light brown or yellow. Eye, ventral surface of body around anus, and pharyngeal and peritoneal linings black. Gill cover usually black but occasionally with a metallic luster (depending on method of preservation); margins of both jaws black. A dark stripe on the mid-dorsal line. Body, especially dorsal half, covered with large black blotches. A fine oblique black line underlying each row of scales, and fine stippling of variable intensity covering the entire body. All fins dusky; the inner ventral fin rays nearly black.

Size. Although this species attains a maximum length of more than 160 mm, the average size of the adult individuals normally caught by bottom trawl is about 115 mm.

Infraspecific Populations. I have referred all western North Atlantic continental shelf collections to *C. agassizi*, a view that may be critized by those who have examined fewer specimens or collections from widely separated localities, for there certainly are recognizable population differences. The western North Atlantic population of *C. agassizi* is composed of many related subpopulations.

At least five infraspecific populations that do not overlap in range can be recognized among the collections made off the continental shelf from New England to Yucatán. Two, the New England and the western Gulf of Mexico populations, are the most distinctive. From north to south, these populations show the following features:

1. ATLANTIC COAST NORTH OF 37°N (Fig. 45 A). Body broader and deeper than in specimens of similar size (about 110 mm) from off the Carolinas. Depth of body at origin of dorsal fin greater than the combined length of snout and eye; depth of caudal peduncle greater than that of the Carolina populations but not of Gulf of Mexico specimens. Width of body at origin of adipose fin about three-fourths of body depth at that point (*cf.* about half in the southern fish). Head, eye, premaxillary and orbit shorter (Table 1).

This form is represented by a series of specimens taken at about 100 fathoms off New York and New England. It includes the type series of *C. chalybeius* (Goode) 1881. I have been unable to determine whether or not eye diameter is correlated with depth of habitat; this form has been taken in shallower water than those farther south. There may be a temperature-controlled depth distribution which secondarily influences the head, eye, and body proportions. I have not been able to study these questions because of a lack of comparable specimens from intermediate localities off the New Jersey-Virginia coast and have considered this form to be infraspecifically related to that from off the Carolinas.

If this northern population is found to be a full species, the name *Chlorophthalmus chalybeius* would be available for it and the distribution of the species provided by Goode would be emended to exclude those specimens taken from south of 37°N. I have examined these southern specimens that have been referred to *C. chalybeius* and have found that they are not identical with the types.

2. Atlantic Coast, from 37°N to Tip of Florida (Fig. 45 b). The less deep and more compressed body and the relatively longer head, premaxillary, and horizontal orbital diameter are characteristic of this population. Depth of body at origin of dorsal fin less than combined lengths of snout and eye; least depth of caudal peduncle less than 7 % of SL; width of body at level of adipose fin about half the depth at this point. Head narrower and shorter, orbit smaller, and interorbital width correspondingly broader than in the northeastern Gulf of Mexico series.

3. Northeastern Gulf of Mexico, from the Straits of Florida North and West to the Mississippi River. Head longer and wider than the Atlantic specimens (especially noticeable in younger specimens); premaxillary and orbit longer. Eye more nearly round and smaller and postorbital head width narrower than in fishes west of the Mississippi. Since the inter-pectoral body width is nearly the same in eastern and western Gulf samples, the flanks of the fish between the eye and the origin of the pectoral fin are parallel in eastern Gulf specimens but converge in the western Gulf.

The northeastern Gulf series differs from that of the eastern part of Campeche Bank, near the Yucatán Channel, in having narrower heads. These two populations are very similar. A series of specimens from off the western end of Cuba may be intermediate in form between the two.

4. Southeastern Gulf of Mexico (Fig. 45c). Only two series of specimens are available. The differences between the eastern Gulf populations are discussed above. This is the most poorly defined population because of a lack of specimens from western Cuba and from the central Campeche Bank.

5. Western Gulf of Mexico (Fig. 45 d). These specimens have larger and more elliptical eyes (especially those from the southwestern Gulf off the Campeche Bank), and less terete but more depressed bodies. Their coloration (in alcohol) is darker than in eastern Gulf specimens, the background being brownish rather than yellow. In all these features, specimens from off the Texas coast more closely resemble eastern Gulf representatives than do those from Campeche.

This form is easily separable from its neighbors to the east. Its habitat includes the continental shelf off Texas and Mexico, from west of the delta of the Mississippi River to somewhere on the Campeche Bank between 87° and 92°W.[7] This population, which seems to vary gradually in a north-south direction within itself, is similar to the few Mediterranean specimens of *C. agassizi* that I have had available.

The apparent break in the distribution of *Chlorophthalmus* off the Mississippi delta may actually indicate a discontinuous distribution and therefore may be of biological significance. This area has been explored. The geographical and consequent morphological criteria that separate the samples from the eastern and western Campeche Bank are harder to evaluate, since few collections have been made there in depths usually frequented by this species. The similarity between western Gulf and European populations separated by easily distinguishable eastern Gulf specimens also suggests environmental influences.

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[7] I know of no collections of *Chlorophthalmus* from the Campeche Bank between these two localities, both Oregon stations.

A few samples of *C. agassizi* are available from Central and South American and Caribbean localities. Although this material does not permit a detailed study, these fish differ from the types already mentioned. The orbit is large, similar in size and shape to the western Campeche Bank form, and the body is darker than in those from farther north.

Development. The eggs and larvae have not been recorded from western North Atlantic collections. Tåning (*30*) has described a series of postlarvae 6.5–25 mm in length and a 46-mm juvenile, all from the Mediterranean. Sanzo (*29*) has figured and described larvae and young, 7.86–30.0 mm in length. All of these larval and postlarval fish were caught near the surface. The size at which metamorphosis and movement to the bottom occurs is not known. The adults are monoecious.

Habits, Distribution and Food. Adults of *C. agassizi* are undoubtedly bottom residents, and they are probably more restricted to this habitat than is the other common and widely distributed western North Atlantic chlorophthalmid, *Parasudis truculentus.* The large number of morphologically separable populations noted above suggest that *C. agassizi* is a nonmigratory bottom dweller. In contrast to the piscivorous *P. truculentus*, *C. agassizi* feeds primarily on invertebrates, many of which are certainly bottom species. All of the adults studied were caught in bottom-trawl or dredge hauls, none in midwater tows. The few records of bottom type associated with catches of *C. agassizi* indicate a preference for mud or clay and, less frequently, for fine sand.

Range. This species is known from the continental shelf of North America from southeast of Nantucket, Massachusetts,[8] south to the coast of Surinam,[9] and at depths of 81–400 fathoms. It is also known from off several of the Caribbean islands. At any given latitude the vertical distribution is broad and appears to be more closely correlated with bottom type and configuration than with depth alone. Although vertical ranges cannot be defined because of the unequal distribution of trawling effort, the upper bathymetric limit, if not the lower, appears to be deeper in the more tropical latitudes. Hence temperature may limit the distribution of the adults. Bottom temperatures are available for 41 of the trawl stations at which *C. agassizi* has been taken. At one of the northern (New England) stations the bottom temperature was 41° F; at another, 42° F. The temperature range of the rest (New England to Yucatán, 95–304 fathoms) was 46°–55° F. The warmer of these temperatures were recorded at western and southern Gulf of Mexico localities.

If the eggs and larvae are pelagic, as they are in the Mediterranean, surface conditions may influence the distribution of the adults.

Synonyms and References:

Chlorophthalmus agassizi Bonaparte, Icon. Fauna Ital., *3* (Pesci), 1840: 2 pp., unnumbered, and pl. ?121, fig. 2 (orig. descr., Mediterranean); O. G. Costa, Fauna Regno Napoli, ... *3* (Pesci) (1844–50) (1), 1845: pp. unnumbered, pl. 35 (descr., color fig., Medit.; Bonaparte, Cat. Metodico Pesci Europei, Naples,

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[8] CARYN St. 14–7, 40°17′N, 67°58′W; a sight record.

[9] OREGON St. 2007, 07°34′N, 54°49′W.

1846: 36 (listed, Medit.); Günther, Cat. Fishes British Mus., 5, 1864: 404 (Messina, juv.); Canestrini *in* Cornalia *et al.*, Fauna d'Ital., 3 (Pesci), 1872: 123 (descr., Medit.); Facciolà, Nat. Sicil., *3* (1883–84), 1884: 71 (juv., Messina); Vinciguerra, Ann. Mus. Civ. Storia nat. Genova, (2) *2*, 1885: 460; Günther, Rep. sci. Res. 'Challenger', Zool., *22*, 1887: 192, pl. 50, fig. c. (Medit. and w. N. Atlantic account; orig. fig.); Carus, Prodr. Faunae Medit. ..., *2*, 1889–1893: 562 (diagn., summary of early Medit. records); Goode and Bean, Smithson. Contrib. Knowl., *30*, 1895: 60, fig. 70 (descr.; ALBATROSS locs.); Jordan and Evermann, Rep. U.S. Fish Comm. (1895), *21*, 1896: 297 (listed; Medit. and e. Atlantic); Jordan and Evermann, Bull. U.S. nat. Mus., *47* (1), 1896: 541 (from Goode and Bean, 1895); Parona, Atti Soc. Ligust. Sci. nat. geogr., Genova, *9*, 1898: 366 (listed); Garman, Mem. Mus. comp. Zool. Harvard, *24*, 1899: 400 (distr.); Weber, Fische 'Siboga'-Exped. ('Siboga'-Exped. Rep. 57), 1913: 79 (depth distr. *cf.* other *Chl.* species); Sanzo, Rend. Accad. Lincei, Rome, (5) *24*, 1915: 462 (notes on 4.5–47 mm pelagic larvae from Messina); Sanzo, Mem. Com. talassogr. Ital., *49*, 1915: 14, pl. 2 (descr. and figs. 5–47 mm juvs. from Messina); Tåning, Rep. Danish oceanogr. Exped. 1908–10, *2* (Biol.) 5, A 7), 1918: 5, figs. 3–4 (Medit. juvs., 6.5–25 mm; dorsal and lateral aspects figured; notes spawning in summer principally in warmer (eastern) part of Medit.); Barnard, Ann. S. African Mus., *21* (1), 1925: 230 (mentioned in account of *C. productus*); Jordan, Evermann and Clark, Rep. U.S. Comm. Fish. (1928), 2, 1930: 165 (listed); Gregory, Proc. Amer. phil. Soc., *23* (2), 1933: 207 (gen. discus., evolution of *Chlorophthalmus* and relatives); Legendre, Ann. Inst. océanogr. Monaco, *14* (6), 1934: 315 (resumé of e. Atl. recs. incl. refs. not repeated here; rec. from tuna stomach, Gulf of Gascogne); Fowler, Bull. Amer. Mus. nat. Hist., *70* (1), 1936: 348 (fig. from Bonaparte; descr. from Italian specimens from Bonaparte coll. in ANSP, said to be types of *C. agassizi*.); Gregory and Conrad, Copeia, 1936: 29 (relationship of Chlorophthalmidae to Iniomi; said to have evolved from the *Sardinioides-Aulopus* line and to have given rise to the Sudidae and Bathypteroidae; generic characterization); Cadenat, Rév. Trav. Off. Sci. Tech. Pêches marit., *10* (4), 1937: 449 (W. coast of Africa, 100–250 m, rec. only); Norman, Sci. Rep. 'John Murray' Exped., 7 (1), 1939: 24 (*cf. C. bicornis*; *C. agassizi* considered ident. with *C. corniger*, *productus* and *proridens*); Walls, Bull. Cranbrook Inst. Sci., 19 (Vert. eye), 1942: 292 (discus. binocular vision); Rey (L. Lozano-), Mem. Acad. Cien. Madrid, Ser. Cien. Nat., *11*, 1947: 374, fig. 112 (descr. 209-mm adult; fig. from Bonaparte, 1840); Tortonese and Trotti, Centro talassogr. Tirreno, publ. 1, 1949: 39 (listed, with Medit. refs.); Smith, Sea Fishes S. Africa (1949), 1950: 115, fig. 184 (*C. productus* referred to *C. agassizi*); Bertin and Estève, Cat. Types Poiss. Mus. Hist. nat. Paris, 6, 1951: 8 (a 70-mm Medit. spec. listed as holotype); Poll, Résult. sci. Exped. océanogr. Belge (1948–49), *4* (2), Poissons, 3, Teleosteens malacopterygiens, 1953: 89 (comp. of *C. atlanticus* with *C. agassizi*, from which it is doubtfully distinct); Zahl, Nat. geogr. Mag., *104* (5), 1953: 601 (color photo., Messina); Kamohara, Jap. J. Ichthyol., *3* (1), 1953: 1 (listed); Dieuzeide, Novella, and Roland, Bull. Trav. Sta. Aquic. Pêche Castiglione, (n. s.) 5 (2, Ostéoptérygiens), 1954: 57 (orig. fig., descr., Algeria); Marshall, 'Discovery' Rep., *27*, 1955: 326 (and elsewhere; discuss. of angle of insertion of pectoral fin and signif.); Dollfus, Trav. Inst. sci. Chérifien, (Zool.) *6*, 1955: 37 (notes species not def. rec. from Morocco); Kamohara, Rep. Usa mar. biol. Sta., *3* (1), 1956: 2 (*cf. C. japonicus*); Kamohara, Res. Rep. Kochi Univ., *5* (15), 1956: 4 (in Jap. with Eng. resumé and key to world species, principally from lit.; *cf.* Japanese forms); Springer and Bullis, U.S. Fish Wildl. Serv., Sp. Sci. Rep. Fish., 196, 1956: 55 (Gulf of Mexico captures by OREGON listed); Denton, Bull. Inst. océanogr. Monaco, *53* (1071), 1956: 6 (light absorption by crystalline lenses of 27 species; lens of *C. agassizi* least absorptive); Tortonese, Iniomi *in* Fauna Flora Golfo Napoli, *38*, 1956: 897, 980 (larvae from Medit., figs. and descr. from lit.; Medit. refs.); Bruun *et al.*, ed., 'Galathea' Deep Sea Exped., 1956: 146 (136 spec. taken off Natal, 550 m); Briggs, Bull. Florida State Mus., Biol. Sci., *8* (2), 1958: 257 (distr.).

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Chlorophthalmus brasiliensis Mead 1959

Figures 44, 46

Study Material. 372 specimens, 58.6–135 mm SL, including the type (from OREGON St. 2082). The species is known only from the five OREGON stations, all off northern Brazil: St. 2080, 02°04′N, 47°00′W, 125 fms., Nov. 17, 1957; St. 2081, 01°52′N, 46°54′W, 175 fms., Nov. 17, 1957; St. 2082, 01°51′N, 46°50′W, 200 fms., Nov. 17, 1957; St. 2083, 01°49′N, 46°48′W, 225 fms., Nov. 17, 1957; St. 2084, 01°45′N, 46°46′W, 275 fms., Nov. 18, 1957. Most of these specimens are in the USNM. Others are in following collections: CNHM, MCZ, ANSP, SU, UMML, BMNH, LMNH, and Stichting Surinaams Museum, Paramaraibo.

Distinctive Characters.[10] The round and tapering form, circular eye of moderate size, and prolonged tip of the lower jaw distinguish *C. brasiliensis* from the western North Atlantic population of *C. agassizi*. The tip of the lower jaw is the most diagnostic feature, for when the mouth is closed its upper face forms a horizontal surface in line

[10] *C. brasiliensis* was compared in greater detail with samples of *C. agassizi* from off Venezuela, British Guiana and Surinam in the type description (Mead, *21*), by using the "ratio-on-size" method for stating proportional differences developed by Parr (*25*, *26*). The length of snout, postorbital width of head, and length of pectoral fin of *C. brasiliensis* were diagnostic for this species, and the following relationships were reported: length of snout, in per cent of prepectoral length, greater than (23.37 + .189 times prepectoral length) (less in *C. agassizi*); postorbital width of head, in per cent of prepectoral length, less than (43.7 + .184 times prepectoral length) (greater in *C. agassizi*); and length of pectoral fin, in per cent of standard length, less than (24.2 + .0086 times standard length) (greater in *C. agassizi*).

with that of the snout (Fig. 46). The snout is relatively longer than that of *C. agassizi* and, in adults, is contained less than 1.3 times in the horizontal diameter of the orbit. This ratio is approached only by the most northern (New England) populations of *C. agassizi*. The diameter of the orbit is less than 40 % of prepectoral length, again a ratio found only in New England varients of *C. agassizi*. *C. brasiliensis* also has a greater average number of anal fin rays (9) than that usually found in *C. agassizi*.

Description. Proportional dimensions in per cent of standard length, based on the range of values for a series of 20 specimens, 93.7–132.0 mm SL.

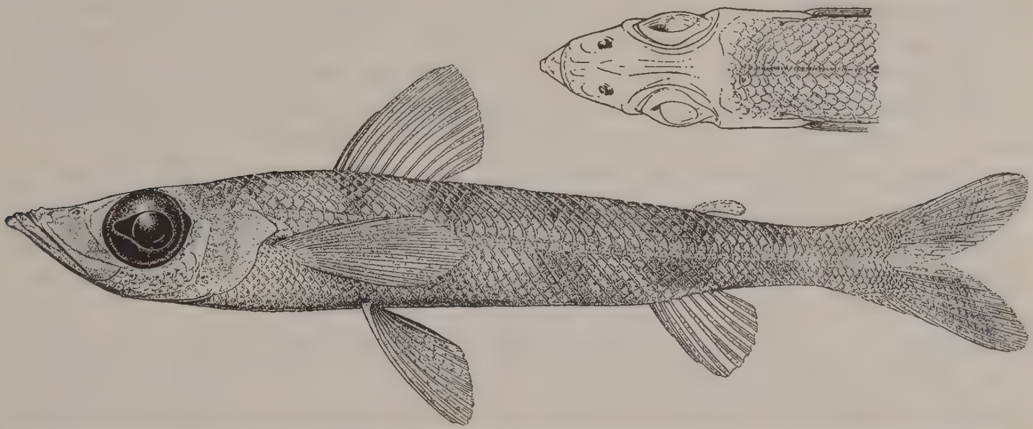

FIGURE 46. *Chlorophthalmus brasiliensis*, 117 mm long, from off northeastern Brazil, OREGON St. 2082, 200 fms., USNM 156892, holotype. Drawn by Margaret G. Bradbury.

Body: depth at origin of dorsal fin 14.2–16.0; of anal fin 10.0–12.2; of adipose fin 8.4–10.6; width close behind bases of pectoral fin 11.5–13.5.

Caudal peduncle: least depth 6.6–7.6.

Head: length 28.7–31.4; width between posterior midpoints of orbits 13.5–14.6; between anterior midpoints of orbits 10.1–11.5.

Snout: length 9.0–10.0; to end of maxillary 12.3–13.7; to tip of lower jaw (mouth closed) 2.2–2.6.

Orbit: horizontal diameter 10.1–11.4.

Bony Interorbital: width 2.7–3.1.

Dorsal fin: length of base 10.3–12.2; depressed height 19.7–23.2.

Anal fin: length of base 6.6–8.0; depressed height 13.5–15.7.

Caudal fin: length of upper lobe from base of first procurrent ray 23.5–26.6.

Ventral fin: length 17.6–20.0.

Pectoral fin: length 22.0–24.7.

Distance from snout to origin of: dorsal fin 35.4–37.8; anal fin 74.5–81.3; ventral fin 39.6–42.6; pectoral fin 28.1–31.5.

Scales: in horizontal series, between upper point of gill opening and base of midcaudal ray 51–56; between anus and origin of anal fin 18–21; along mid-line anterior to dorsal fin 13 or 14; rows between origin of dorsal fin and lateral line 7 or 8.

Gill rakers: on lower limb of first arch 20–23 (usually 21); total count on first arch 23–26 (modally 24).

Fin rays: dorsal 11; anal 9 (occasionally 8 or 10); caudal 1-17-1; ventral 9; pectoral 16 or 17.

Vertebrae: 48 or 49, including hypural.

BODY nearly circular in cross section anteriorly but becoming compressed posteriorly; its depth at dorsal origin 1.9–2.2 in hl, its width immediately behind insertion of pectoral fin 2.3–2.8 in hl.

SCALES covering body and suborbital region of head; the scales deciduous, imbricate, weakly denticulated and cycloid. No prominent axillary scales; those surrounding pelvic base and those in and below the axil of the pectoral fin little larger than body scales and variously shaped. Fins without scales except for bases of caudal rays. LATERAL-LINE scales pierced by a tube but otherwise similar to body scales.

HEAD broadest immediately behind eye; its sides converging evenly forward to the rounded snout; its length 3.2–3.5 in SL; the lower jaw terminal. Tip of SNOUT on a horizontal with center of eye and with tip of lower jaw, when the mouth is closed; length of snout 1.1–1.2 in diameter of orbit. Head covered by an extensive network of SENSORY PORES that cannot be described satisfactorily because of the loss of skin from all specimens. This system is most highly developed on the interorbital region; particularly evident are the pores that extend onto the dermal dorsal eyelid, those of the circumorbital system, and the scattered series of pores on the ventral surface of the head.

GILL RAKERS on first arch flattened and of moderate length, the longest longer than the gill filaments opposing it and about equal to the diameter of the pupil; rakers on second arch similar but shorter; those on the last two arches reduced to spine-bearing knobs.

Angle of gape just before a vertical from anterior edge of orbit. UPPER JAW bones (maxillary and premaxillary) ending below anterior edge of pupil; posterior 0.67 of maxillary surmounted by a long and slender supramaxillary; maxillary broad posteriorly, its rear edge sloping downward, forward and inward. LOWER JAW terminal, extending beyond the upper and ending in a horizontal triangular plate; this mandibular extension (snout to tip of lower jaw with mouth closed) 3.5–4.2 in length of snout. Tip of tongue free.

The extreme tip of the lower jaw, distal to the symphyseal ridge with its adjacent tooth patches, is pierced by a pair of pores, each forming an entrance to a bony tube leading to the lower surface of the mandible near its tip. These channels continue posteriorly, median to the lower edge of the rami of the mandible, passing through at least two pairs of ossified tunnels. Because of skin loss, it is impossible to determine whether or not this channel, after it emerges from the bone, is a completely enclosed tube; there are no remnants of such a tube between the ossified tunnels.

TEETH present on premaxillary, dentary, palatine and vomer; none on tongue.

Teeth present on terminal part of lower jaw but not at the extreme tip; a pair of tooth-bearing patches lateral to the toothless median symphyseal ridge; the teeth small, bristle-like, and depressible; these patches not continuous with the principal series of mandibular teeth, which are minute, depressible, needle-like and recurved, and form a band that decreases in width posteriorly. The premaxillary teeth are minute, of about equal size, slightly recurved, depressible and form a narrow band. Anteriorly this band is on the ventral surface of the premaxillary; posteriorly it is on the lateral surface. The two lateral knobs of the vomer bear patches of stronger teeth, most of which are depressible. Though widely separated, these patches are continuous with one another, in most specimens, by way of a single row of minute teeth along the anterior edge of the vomer. The palatine teeth are very small and are restricted to a band along the anterior half of that bone.

DORSAL and ANAL fins with first 3 rays unbranched, the third longest, their depressed heights 1.3–1.5 and 2.0–2.2 in hl, respectively. Predorsal distance 2.6–2.8 and the preanal distance 1.2–1.3 in SL. VENTRAL and PECTORAL fins 5.0–5.7 and 4.0–4.5 in SL, respectively; the preventral distance 2.3–2.5, the prepectoral distance 3.2–3.6, in SL.

Color. In preservative, background color of body yellowish or occasionally orange; nearly white ventrally, becoming brownish dorsally in fresh specimens. The irregular dark blotches below midline more prominent in young than in old specimens. Broad vertical bands of variable width dorsally. Viewed from above, the most prominent ones are at the nape, at each end of the base of the dorsal fin, midway between dorsal and adipose fins, just ahead of the adipose fin, midway between adipose fin and procurrent caudal rays, and through these procurrent rays; narrower bands between these; the pattern, rather variable, fading with preservation in alcohol. Tip of lower jaw and edge of upper jaw, operculum, linings of pharyngeal and abdominal cavities, eye and anus black. Snout and top of head dusky. Suborbital, and to a lesser extent the ventral surface of head and body, stippled. A black stripe extending along entire mid-dorsal line, most conspicuous between the nape and origin of dorsal fin. The scale rows delineated by black lines. Fins dusky.

Size. All known specimens are between 58 and 135 mm long.

Range. C. brasiliensis is known only from five OREGON stations off northern Brazil; 125–275 fathoms (see *Study Material*, p. 176, and Fig. 44).

Reference:

Chlorophthalmus brasiliensis Mead, J. Wash. Acad. Sci., *48*, 1959: 362, fig. 1 (orig. descr.; off Brazil; *cf. C. agassizi*).

Genus *Parasudis* Regan 1911

Parasudis Regan, Ann. Mag. nat. Hist., (8) 7, 1911: 127; type species, by monotypy, *Chlorophthalmus truculentus* Goode and Bean, Smithson. Contrib. Knowl., *30*, 1895: 61; Barbados.

Characters. Snout longer than in *Chlorophthalmus*, spatulate and depressed, longer than wide. Upper jaw bones reaching nearly or quite to anterior edge of orbit. Posterior part of head and body anterior to ventral fins about as broad as deep. Gill flap extending beyond upper end of insertion of pectoral fin. Dorsal fin originating in advance of ventral fin. Anus unpigmented, located in second third of the distance from insertion of outer ventral ray to insertion of anal fin, and separated from bases of inner ventral rays by 8–10 rows of scales. Teeth on jaws, palatines and vomer; palatine teeth larger than those in jaws; a pair of large fixed canine teeth on vomer and a broad band of depressible teeth on the palatines; some teeth on tip of mandible directed forward. Gill rakers of moderate length, 10–14 on lower limb of anterior arch, those near angle shorter than the opposing gill filaments. Fewer than 40 vertebrae.

Range. Tropical eastern Atlantic; tropical and temperate western North Atlantic.

Species. There are two nominal species, *Parasudis truculentus* (Goode and Bean) and *P. fraser-brunneri* (Poll). The latter species, a tropical eastern Atlantic form which may be conspecific with *P. truculentus*, is discussed on page 183.

Parasudis truculentus (Goode and Bean) 1895

Longnose Greeneye

Figures 44, 47

Study Material. Several hundred western North Atlantic specimens, 80.0–224.5 mm SL, in USNM, MCZ, CNHM, UMML, TU, BLBG, and UF. The localities of these collections are indicated in Fig. 44.[11]

A comparison of this western North Atlantic series with the African *Parasudis fraser-brunneri* was made possible by Max Poll of the Musée Royal du Congo Belge, Tervuren, Belgium, who generously supplied three paratypes of that species.

Distinctive Characters. The generic characters distinguish this species from related western North Atlantic forms.

Description. Proportional dimensions in per cent of standard length, based on 20 specimens, 97.4–196.0 mm SL, from the northern and southern Gulf of Mexico and from off the coasts of Surinam and Brazil.

Body: depth at origin of dorsal fin 14.9–18.4; at origin of anal fin 10.3–12.9; width at base of pectoral fins 10.9–14.4.

Caudal peduncle: least depth 7.1–8.4.

Head: length 31.6–33.9; width between midposterior points of orbit 12.1–13.3.

Snout: length from tip of upper jaw to nearest point of eye 12.5–13.6; to end of maxillary 12.1–14.3.

Orbit: horizontal diameter 10.2–11.9; vertical diameter 8.0–9.4.

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[11] The most northern specimens, from south of Nantucket, Massachusetts, were collected during the course of the exploratory work of the CAP'N BILL II. Those from off the Atlantic coast of Florida, Georgia and the Carolinas were caught by the U.S. Fish and Wildlife Service vessels PELICAN and COMBAT and those from the British and Dutch West Indies by the U.S. Fish Commission steamers BLAKE and ALBATROSS. The remainder were taken by the U.S. Fish and Wildlife Service exploratory vessel OREGON.

Eye: horizontal diameter 8.9–10.5; vertical diameter 7.6–9.0.

Bony interorbital: width 2.6–3.3.

Dorsal fin: length from origin to tip of longest ray when depressed 19.2–21.5.

Anal fin: length from origin to tip of longest ray when depressed 13.3–15.4.

Caudal fin: length from base of middle ray to end of upper lobe 19.5–22.7.

Ventral fin: length 18.8–20.9.

Pectoral fin: length 20.6–24.2.

Distance from snout to origin of: dorsal fin 39.9–43.0; anal fin 77.9–80.8; ventral fin 44.4–48.3.

Distance from origin of dorsal fin to origin of: adipose fin 39.5–42.3; anal fin 39.0–42.3.

Scales: 78–85 in a longitudinal series above the lateral line from gill opening to base of caudal.

Gill rakers: 1 + 11 to 1 + 13.

Fin rays: dorsal 10; anal 9; caudal 1-17-1; ventral 9; pectoral 15 or 16.

Vertebrae: 38.

BODY compressed; head, behind eye, about circular in cross section; snout depressed and spatulate. Ventral contour nearly straight from tip of lower jaw to origin of anal fin. Dorsal outline sloping upward without notable curvature from snout to deepest point of body, at origin of dorsal fin. Beyond this point, the dorsal and ventral outlines converge gradually to the rather stout caudal peduncle, the ventral outline turning more abruptly upward at origin of anal fin. Depth of body at origin of dorsal fin 5.4–6.2 in SL; its depth at origin of anal fin 2.5–3.3 in hl. Least depth of CAUDAL PEDUNCLE 4.0–5.0 in hl.

SCALES on body, suborbital and postorbital regions of head, and base of caudal fin, strongly adherent and imbricate; those on body cycloid but bearing weak serrations along the distal edge; scales on caudal base small and decreasing in size posteriorly. Snout, interorbital and opercular regions, and paired fins naked. No elongate axillary scales; those beneath the pectoral slightly larger than those adjacent, but of similar shape. Larger scales also overlying the insertion of the ventral side of ventral fins; also a few similar scales behind the origins of inner ventral rays. LATERAL-LINE scales have the anterior edge lengthened, the scales more deeply inserted than those above and below, which have a nearly straight anterior edge; last scale overlying the base of mid-caudal ray.

HEAD 2.9–3.2 in SL. SNOUT broad and rounded anteriorly, its length 2.4–2.6 in hl; the lower jaw protruding slightly, terminating anteriorly with the symphyseal knob. ORBIT horizontally elongate, the anterior and posterior midpoints laterally produced to form bony knobs, its horizontal diameter 2.8–3.3 in hl. EYE slightly longer than high, 3.2–3.6 in hl. IRIS keyhole-shaped. INTERORBITAL space narrow, its least bony width 3.1–3.6 in horizontal diameter of eye. Circumorbital dermal covering with many transverse mucous or SENSORY PORES, forming a part of the well-developed system covering most of the nonscaled parts of head.

GILL RAKERS well developed, the longest on the first arch about equal to the greatest width of premaxillary and a little shorter than the gill filaments opposite it; their outer surface smooth, the inner surface toothed.

GAPE long, about two thirds of the length of snout. MAXILLARY expanded posteriorly, extending to or beyond (especially in the young) a perpendicular from the anterior edge of orbit, its posterior half surmounted by a supramaxillary; its posterior edge running obliquely downward and forward, the flattened posterior surface of the bone not in a vertical plane but sloping inward ventrally.

TEETH on anterior part of mandible forming two rows, both rows outside of the mouth when jaws are closed; the posterior row with recurved, depressible, conical teeth directed upward and slightly outward; the anterior row consisting of blunt, conical teeth directed forward. Symphysis with a strong bony knob. Posterior to these two rows, a band of recurved, conical, depressible teeth, the inner ones longest and strongest; the outer ones shorter but of similar form, the band becoming narrower posteriorly. Symphysis of upper jaw toothless. Premaxillary toothed for almost its entire length, this broad band similar to that on the mandible, the teeth also depressible but smaller. Vomer bearing two strong, recurved, conical and immovable fangs, one at each lateral edge of the bone. These are set in firm bony sockets that rise above the surface of the bone and are especially strong along the anterior face of the tooth. Anterior half of palatine with a broad band of recurved depressible teeth; the innermost strongest. Tip of TONGUE free, the end rounded and bearing minute stiffened papillae.

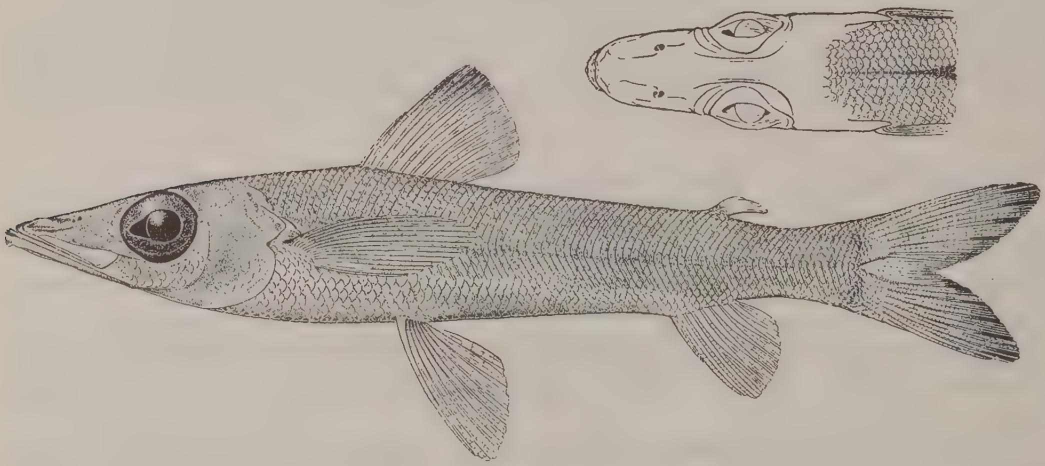

FIGURE 47. *Parasudis truculentus*, 168.5 mm long, from the Campeche Bank, OREGON St. 1055, 225 fms., USNM 185678. Drawn by Margaret G. Bradbury.

DORSAL fin with first 2 rays unbranched, the 3rd and 4th longest and of about equal length; its height from origin to tip of longest ray when depressed 1.6–1.7 in hl; predorsal distance about equal to distance between origins of dorsal and adipose fins, 2.2–2.5 in SL. ANAL fin with 3 branched rays, the 3rd longest, its height when depressed 2.2–2.5 in hl; preanal distance 1.2–1.3 in SL; distance from origin of dorsal fin to origin of anal 2.4–2.6 in SL. Lobes of CAUDAL fin of about equal length, the fin forked. VENTRAL fin with 1st ray unbranched; the 2nd ray, or 1st branched ray, the longest; its length 1.6–1.9 in hl; preventral distance 2.1–2.2 in SL. PECTORAL fin long and pointed, its origin below the end of opercular flap.

Color. In alcohol, background color light brown, darker above than below. The edge of each row of scales indicated by a black line on the underlying skin; the lateral line reddish. Suborbital region, mouth, jaws, and subopercular lining without pigment. Top of snout and linings of opercular bone, pharynx, esophagus, stomach and abdominal cavity black. Tip of dorsal fin black; pectoral fin dark gray; ventral, anal and adipose fins very lightly pigmented. Fork of caudal fin lined with black, the remainder dark grey or black. The young (under about 80 mm) frequently have several broad vertical dark bands on the body.

The bodies of fresh specimens are uniformly light brown above with white bellies and dark vertical fins. In life, the tapetum of the eye reflects a bright iridescent green.

Size. This species attains a length of 225 mm.

Habits. Little is known about the habits or life history of the longnosed greeneye. The eggs and larvae of *P. truculentus* are unknown. The spawning season is probably in early spring, for the ovaries of those caught on the Campeche Bank were developing in December, ripe in May, and spent later in the season. The spawning season is earlier in the Caribbean, for specimens from south of Curaçao which were caught in February had recently spawned. Those from off the coasts of Brazil and the Guianas were ripe in November.

This species is hermaphroditic. A cross section of the ovotestis reveals well-developed mature testicular and ovarian tissue. The ovary becomes mature when the fish attains a standard length of about 145 mm. The reproductive system and breeding behavior are unknown.[12]

The strong jaw and palatine teeth and the heavy immovable vomerine fangs suggest that *P. truculentus* is a voracious feeder, and an examination of stomach contents indicates that it feeds in midwater above the bottom. In contrast to the stomachs of *Chlorophthalmus agassizi*, which most commonly contained benthonic crustacea and molluscs, the stomachs of *P. truculentus* contained principally fishes and, less frequently, squids. Most of the fishes belonged to two groups; lantern fishes (Myctophidae) and *Maurolicus*-like gonostomatids. The long and narrow stomachs of *Parasudis* can expand to the full length of the abdominal cavity, and one such stomach contained the headless body of a fish which, in life, was about one-third the length of its captor.[13]

Relationships. There are two nominal Atlantic species of this genus: *Parasudis truculentus* (Goode and Bean) 1895 and *P. fraser-brunneri* (Poll) 1953. The first of these was described from a single specimen about eight inches in length taken at a depth of 158 fathoms off Barbados.[14] This type specimen cannot be found, and although I have referred all of the western North Atlantic material to *P. truculentus*, this allocation is open to question. The three available specimens from the type locality do not correspond in every detail with Goode and Bean's account. These authors recorded dorsal and anal fin-ray counts of 9 and 8 respectively, while all of the western Atlantic specimens provide counts of 10 and 9 respectively. Additional differences are apparent when morphometric data, taken largely from Goode and Bean's figure,[15] are compared with those from the present series. Their fish was described as having a slightly larger eye (11.0 % of SL. *cf.* 9.7–10.1 % in Barbados specimens) and a correspondingly larger orbit (12.7 % *cf.* 11.0–11.7), a shorter preanal length (79.0 *cf.* 79.9–81.0) and a shorter preventral length (46.0 *cf.* 47.5–50.9). The lower jaw of their fish projected beyond the upper by a distance equal to one-fourth (according to the description) or one-sixth (shown on the figure) of the length of the snout, while in our material this ratio is about one-eighth. Finally, the upper jaw bones (maxillary and premaxillary) do not reach a perpendicular from the anterior rim of the orbit, while in our Barbados specimens they reach to, or slightly beyond, such a perpendicular. There is considerable geographical variation in the length of the upper jaw bones.

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[12] Thousands of individuals, in spawning condition, have been seen off the northeastern coast of South America (Mead, *22*).

[13] These notes are based on the laboratory study of about 20 specimens from the Campeche Bank, Gulf of Mexico, and on the examination of several hundred fresh individuals which were trawled by the OREGON during her exploratory work along the coasts of Brazil and the Guianas in November, 1957.

In the absence of the type specimen, all western North Atlantic specimens are here referred to the single species *P. truculentus*.

A comparison of three paratypes of the eastern Atlantic *P. fraser-brunneri* with the northwestern Atlantic specimens shows that this species is distinct from *P. truculentus*, but the differences are slight. Measurements were possible on two of these three paratypes (143.5 and 155.5 mm SL). These have longer heads, snouts, premaxillaries, pectoral fins, and ventral fins than the western Atlantic *P. truculentus*.[16] The origin of the dorsal fin in *P. fraser-brunneri* is also slightly in advance of the midpoint between the snout and the origin of the adipose fin rather than at this midpoint. These two species are apparently identical in other respects.

P. truculentus is also of interest because of its relationship to the iniomous fishes of the Suborder Alepisauroidea. In many ways it is more similar to such fishes as the paralepidids than is any other benthonic myctophoid with the possible exception of *Scopelosaurus* (see Regan, *28*). These similarities suggest a phylogenetic relationship, but they may merely reflect parallel adaptions to a midwater environment. It has been pointed out that *P. truculentus* is piscivorous and that it probably feeds above the bottom.

Relation to Man. The longnose greeneye is of no current value to man. Should an offshore fishery develop for shrimp and associated fishes, *P. truculentus* may form a substantial element in the "trash fish" catches. The flesh is white and palatable, the flavor being similar to that of the smelts, but since the body is soft, its future as a foodfish is not a bright one.

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[14] BLAKE St. LII.

[15] The use of measurements taken from a figure (*12*) is admittedly unprecise.

[16] Respectively, 34.4–35.0, 13.9–14.3, 14.4–14.6, 24.2–24.4, and 21.0–21.9 % of SL compared with these proportional measurements taken from the northwestern Atlantic specimens: 31.6–34.2, 11.6–13.6, 12.1–14.3, 20.6–24.3, and 16.0–20.9 %.

Abundance. Prior to the use of commercial trawls in deep-water shrimp exploration, the species was known from few specimens and was considered a rarity. The descriptions of the collections obtained off tropical West Africa by the Belgian Oceanographic Expedition showed that the African *P. fraser-brunneri* was a common species in offshore waters there. Later American explorations, especially those of the vessels OREGON, PELICAN and COMBAT, showed that our *P. truculentus* is a common offshore resident. Hundreds of individuals are frequently caught in one-hour drags of a 40-foot trawl.

Range. P. truculentus is known from Nantucket, Massachusetts, south to the Gulf of Mexico, off St. Kitts and Barbados, south of Curaçao, and from several other Caribbean and South American localities. These records, plotted in Fig. 44, include several sight-records made in the Gulf of Mexico by the staff of the OREGON.[17] Because of the unique appearance of this species, I consider these sight records reliable.

Depth, bottom temperature, and type of bottom seem to be factors limiting the distribution of the species. All of the known captures of *P. truculentus* have been in bottom trawlings made at depths of from 100–262 fathoms, with bottom sediments of mud or, occasionally, mud mixed with sand or bits of coral, and with bottom temperatures of 48°–56° F. No *P. truculentus* has been found above the bottom. It has been caught on the bottom at all hours. This suggests that its excursions into the midwater range, which the food habits indicate, are not correlated with time of day.[18]

Synonyms and References:

Chlorophthalmus truculentus Goode and Bean, Smithson Contrib. Knowl., *30*, 1895: 61, fig. 72 (orig. descr., Barbados); Jordan and Evermann, Rep. U.S. Fish Comm. (1895), *21*, 1896: 297 (listed); Jordan and Evermann, Bull. U.S. nat. Mus., *47* (1), 1896: 542 (from Goode and Bean, 1895); Garman, Mem. Mus. comp. Zool. Harvard, *24*, 1899: 400 (distr.); Jordan, Evermann and Clark, Rep. U.S. Comm. Fish. (1928), 2, 1930: 165 (listed); Longley and Hildebrand, Publ. Carnegie Inst. Wash., 535, 1941: 26 (recorded from south of Tortugas, Fla.; 180–220 fms.); Kamohara, Jap. J. Ichthyol., *3* (1), 1953: 2 (listed); Poll, Résult. Sci. Expéd. océanogr. Belge (1948–49), *4* (2), 1953: 94 (*cf. P. fraser-brunneri*); Schroeder, Deep-Sea Res., *3*, Suppl., 1955: 362 (distr. off New England); Kamohara, Res. Rep. Kochi Univ., *5* (15), 1956: 3, pl. 1, fig. 3 (from Goode and Bean, 1895); Springer and Bullis, U.S. Fish Wildl. Serv., Sp. Sci. Rep. Fish., 196, 1956: 55 (Gulf of Mexico rec. of capture by OREGON); Briggs, Bull. Florida State Mus., Biol. Sci., *8* (2), 1958: 257 (distr.).

Parasudis truculentus, Regan, Ann. Mag. nat. Hist., (8) 7, 1911: 128 (*cf. Chlorophthalmus* and *Paralepis*).

Chlorophthalmus (*Parasudis*) *truculentus*, Parr, Bull. Bingham oceanogr. Coll., *3* (3), 1928: 18 (from Goode and Bean, 1895).

Genus *Bathysauropsis* Regan 1911

Bathysauropsis Regan, Ann. Mag. nat. Hist., (8) 7, 1911: 127; type species, by monotypy, *Chlorophthalmus gracilis* Günther, Ann. Mag. nat. Hist., (5) *2*, 1878: 182; eastern coast of New Zealand.

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[17] One such record is excluded, since the data from OREGON St. 1088 differ so greatly from those pertaining to other capture records for this species that the record is questionable.

[18] *P. fraser-brunneri*, the close trans-Atlantic relative of our species, shows similar depth, bottom, and temperature preferences (*5*; *27*).

Generic Synonym:

Bathysaurops Fowler, Proc. U.S. nat. Mus., *85*, 1938: 31; type species, by monotypy, *Bathysaurops malayanus* Fowler, 1938; Gulf of Boni, Celebes, Dutch East Indies, 484 fms.

Characters. Snout depressed. Interorbital space broad, its width greater than vertical diameter of eye. Upper jaw bone (maxillary) extending beyond posterior edge of iris. Gill rakers of the usual lath-like form, those near the angle of the first arch longer than the gill filaments opposite them. Gill arches extending forward into mouth beyond angle of gape. Origin of ventral fin in advance of origin of dorsal fin. Anus located closer to origin of anal fin than to origins of ventral fins. A single series of teeth on vomer and palatine bones, the vomerine series interrupted in the middle. Some teeth on roof of mouth barbed. Palatine teeth longer than those in jaws.

Range. The species of *Bathysauropsis* are known from deep water (1100–1425 fms.) in the temperate and tropical latitudes of the South Atlantic and South Pacific oceans.

Species. There are three named species: *B. gracilis* (Günther) from the South Atlantic and South Pacific, *B. malayanus* (Fowler) from the Philippine Islands, and *B. gigas* Kamohara (*17*) from Japan. None of these is known to occur in the western North Atlantic, and *Bathysauropsis* would have been excluded from these volumes entirely were it not for its critical and interesting phylogenetic position intermediate between the archibenthic chlorophthalmids and the abyssal-benthic ipnopids and bathypteroids. In position and shape of fins, scalation, shape and structure of lower jaw, small tongue, anterior extent of gills, large mouth and general appearance these fishes are quite similar to *Ipnops*. On the other hand, the large eye, the number of branchiostegal rays[19] and the extent and pattern of the teeth are suggestive of *Chlorophthalmus*. Two species have 9 ventral fin rays, as in all chlorophthalmids, while another (*B. gracilis*) has but 8, the usual ipnopid number. It is also of interest that *B. gracilis*, which is known only from depths greater than 1000 fathoms and which is clearly a benthonic form, has the large eye of a *Chlorophthalmus* rather than the minute or vestigial eye characteristic of most other abyssal-benthic inioms.

The generic diagnosis given above will separate *B. gracilis* from all other western North Atlantic iniomous fishes. References to *B. gracilis*, the only known Atlantic species, are noted below.

Synonyms and References:

Chlorophthalmus gracilis Günther, Ann. Mag. nat. Hist., (5) *2*, 1878: 182 (descr.; E. coast of New Zealand, Juan Fernandez, central S. Atlantic; 1100, 1375, 1425 fms.; 5 spec. 4–9.5 inches long); Günther, Rep. sci. Res. 'Challenger', Zool., *22*, 1887: 194, pl. 49, fig. A (redescr. CHALLENGER specs.); Garman, Mem. Mus. comp. Zool. Harvard, *24*, 1899: 400 (distr.); Gilchrist, Mar. Invest. S. Africa, *4*, 1906: 165 (rec. 2 spec. caught off Cape Point, S. Africa; 755 fms.); Waite, Rec. Canterbury (N.Z.) Mus., 1 (1), 1907: 13 (listed); Gilchrist, Mar. Invest. S. Africa, *4*, 1908: 165 (755 fms., 38 mi. N.E. by E. of Cape Point);

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[19] Usually 8 (4+4) branchiostegal rays in both *Chlorophthalmus* and *Parasudis*, the same number as are present on the type specimen of *B. malayanus*. I have not seen either of the other species of *Bathysauropsis*.

Gilchrist and von Bonde, Rep. Fish. Mar. Biol. Surv. Union S. Africa, *3* (1922), 7 (2), 1924: 7 (distr.; Cape Point, S. Africa; 600–1220 fms.); Fowler, Monogr. Acad. nat. Sci. Philad., *6*, 1944: 489 (listed; on Günther's CHALLENGER recs.).

Bathysauropsis gracilis, Regan, Ann. Mag. nat. Hist., (8) *7*, 1911: 126 (*cf. Chlorophthalmus* and the Bathypteroidae); Waite, Rec. Canterbury (N.Z.) Mus., *1* (3), 1911: 166 (Günther's CHALLENGER descr. *cf. Chlorophthalmus nigripinnis*); Barnard, Ann. S. African Mus., *21* (1), 1925: 230 (descr., spec. up to 320 mm caught by the PIETER FAURE off Cape Point and Table Bay; 475–1220 fms.); Parr, Bull. Bingham oceanogr. Coll., *3* (3), 1928: 18 (diagn., in key and synonymy); Smith, Sea Fishes S. Africa (1949), 1950: 185 (diagn. and fig.); Marshall, 'Discovery' Rep., *27*, 1955: 326 (angle of insertion of pectoral fin and signif.).

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Family Ipnopidae

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Characters. SLENDER BOTTOM FISHES OF THE DEEP SEA AND ADJACENT PARTS OF THE CONTINENTAL SLOPE WHICH, AS ADULTS, ARE ABOUT 4–18 INCHES LONG. Body round in cross section anteriorly but with slightly flattened ventral surfaces; compressed posteriorly. Snout depressed and spatulate (as in the Bathypteroidae) in *Ipnops* and *Bathymicrops*, or more rounded (as in *Aulopus*). Eye broad, flat, dorsally directed, and lensless (*Ipnops*), or minute, vestigial, and wholly or partly covered by skin and scales.

Scales present on cheeks, sides of head, body, and base of caudal fin; the scales usually completely lost; top of head with or without scales. Lateral line terminates at base of midcaudal rays.

Dorsal fin in anterior half of body, its base shorter than length of head, the fin formed of 9–13 rays. Anal fin posteriorly placed, its origin farther behind end of base of dorsal fin than the origin of the dorsal is behind that of the ventral fin; base of anal fin longer than that of dorsal, shorter than head in *Bathytyphlops*, about equal to length of head in *Ipnops* and *Bathymicrops*; the fin composed of 13–16 rays. Caudal fin long, with a shallow fork, the lobes equal, the fin usually composed of 19 (1-17-1) principal rays (see ftn. 15, p. 155). Ventral fins with 8 rays, inserted well in advance of dorsal, and without prolonged rays, the fins lying in an oblique plane when expanded. Pectoral fins undivided and of variable lengths, with 9–16 rays. No adipose fin.

Anus closer to insertion of ventral fin than to origin of anal fin. Anal papilla moderately well developed.

No luminous organs (see p. 150).

Lower jaw terminal, the tip turned slightly upward. Upper jaw longer than half the length of head, extending well beyond eye in *Bathymicrops* and *Bathytyphlops*. Maxillary dilated and compressed posteriorly, or splint-like and without an expanded posterior end. One elongated supramaxillary or none.

Reprinted from Memoir Sears Foundation for Marine Research, I (5), 1966: 147–161.

No tongue; the glossohyal bone reduced and bound, in an oblique position, to the basihyals.

Teeth on jaws, on vomer, and usually on the palatines; teeth minute and needle-like, mostly depressible and none enlarged into the lanceolate or canine type.

Gill arches extending far forward into the mouth. Gill rakers either lath-like and of the usual appearance, or reduced to low rugose knobs with only that at the angle of the arch of normal appearance. Pseudobranchiae absent. Gill opening and gape large. Branchiostegal membranes free from each other and from the isthmus, covered anteriorly by a well-developed transverse gular fold, and extending posteriorly beyond opercular flap. Branchiostegal rays 10–17, of which 4 originate on the epihyal.[1] Opercular flap firm, the posterior edge formed by the operculum and the suboperculum. Interopercle well developed.

Vertebrae 53–64.[2]

Remarks. All ipnopids are archibenthic or abyssal-benthic, and one species or another has been found in each of the major oceans.

No more than about 40 ipnopid specimens are known. There is no published information on the life history or behavior of any, but the unusual structural modifications suggest unique modes of existence. *Ipnops* (p. 149) is thought to rest on the bottom on its flattened ventral surface and horizontally oriented ventral fins. *Bathymicrops regis*, which is similar in form to *Ipnops*, has no cephalic photoreceptor and has none of its other organs of perception notably well developed. Structural loss has proceeded even further in *Bathytyphlops marionae*, for this species is not only blind, as is *Bathymicrops*, but its teeth are reduced to minute denticles, which form rugose plates or grinders on most of the bones that line the mouth, while its gill rakers, except for the one at the angle of the first arch, are reduced to low tooth-bearing plates. No explanation for these structural losses and modifications has been proposed.

Among the myctophoid inioms, *Ipnops* and *Bathymicrops* are the most closely related to the Bathypteroidae and possibly arose from a form intermediate between this family and a chlorophthalmid similar to *Bathysauropsis gracilis* (p. 185). Of the ipnopid genera, *Ipnops*, in spite of the specialized cephalic organs, is more similar to *Bathypterois* than are either *Bathymicrops* or *Bathytyphlops*. Several characters are shared by *Ipnops* and *Bathypterois*: the flattened and naked frontal bones that roof the head, the row of pores and cavernous bones that lie between the upper jaw and the edge of the frontal, the jaw structure and shape of the premaxillary and supramaxillary, the shape of the body, and the placement of the fins.

Genera. Three ipnopid genera are currently recognized, and all are represented in the western North Atlantic. The relationships among these three, *Ipnops* Günther 1878, *Bathymicrops* Hjort and Koefoed 1912, and *Bathytyphlops* Nybelin 1957, have not been determined, and the family may not be a natural group. In form of head, jaws, and development of eyes and gill rakers, *Bathymicrops* is intermediate between *Ipnops* and the deeper-bodied *Bathytyphlops*. The reduced upper jaw bones, high number of branchiostegal rays (15–16) and the vestigial gill rakers of *Bathytyphlops* are, however, suggestive of the Synodontidae. Further comparative studies may indicate that *Bathytyphlops* represents a distinct family intermediate between the Ipnopidae and the Synodontidae.

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[1] From specimens of *Ipnops* and *Bathytyphlops* and published accounts of *Bathymicrops*.

[2] From western Atlantic specimens of *Ipnops murrayi*, types of *I. pristibrachium*, *Bathytyphlops marionae*, *B. sewelli*, and *Bathymicrops regis*.

Key to Genera

1 a. Top of head without scales, roofed by broad, thin and flattened bones; no laterally directed eye above upper jaw. *Ipnops* Günther 1878, below.

1 b. Top of head with scales; a minute laterally directed eye immediately above upper jaw.[3]

  2 a. Gill rakers on first arch of the usual lath-like shape; greatest depth of body more than 10 in SL; 9–10 pectoral fin rays; 9 or 10 dorsal fin rays. *Bathymicrops* Hjort and Koefoed 1912, p. 154.

  2 b. Gill rakers on first arch, except for that at angle, reduced to low rugose knobs or discs; greatest depth of body about 6 in SL; 11–13 pectoral fin rays; 11–14 dorsal fin rays. *Bathytyphlops* Nybelin 1957, p. 157.

Genus *Ipnops* Günther 1878

Ipnops Günther, Ann. Mag. nat. Hist., (5) *2*, 1878: 186; type species, by monotypy, *I. murrayi* Günther 1878; type locality, as restricted by Grey (5), CHALLENGER St. 133, Atlantic near Tristan da Cunha, 3475 m.

Generic Synonyms:

Lychnoculus Murray, Manchester Sci. Lect., 9, 1877: 132; type species, by monotypy, *L. mirabilis* Murray 1877;[4] no type locality given.

Ipnoceps Fowler, Bull. U.S. nat. Mus., *100* (14, pt. 2), 1943: 56; type species, by monotypy, *I. pristibrachium* Fowler 1943; western Pacific, Gulf of Tomini, 1992 m.

Characters. Slender fishes with depressed, spatulate snouts. Body with greatest depth more than 10 in SL. Head without scales on upper surface and roofed by a pair of large transparent membrane (frontal) bones covering a photoreceptive organ which is bright yellow in life (see ftn. 6) and which is longitudinally divided into two symmetrical halves. Teeth villiform and in bands on both jaws; a patch of minute teeth on vomer; and a few exceedingly small teeth on palatine. Maxillary expanded posteriorly and similar in shape to that of *Bathypterois*. Gill rakers of the usual lath-like form and of moderate length. Anus located immediately behind bases of ventral fins. Dorsal fin origin behind a vertical from anus. Anal fin originates posteriorly, its base long. Color of body dark, the edges of the scale pockets without pigment.

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[3] The original description of *Bathytyphlops sewelli* includes the statement that the eyes are vestigial or absent, and no eye is shown on the figure of the type. N. B. Marshall of the British Museum (Natural History) has generously re-examined the type for me; the eyes are best referred to as vestigial, not absent.

[4] An appeal for the suppression of the generic and specific names *Lychnoculus mirabilis* has been submitted to the International Commission on Zoological Nomencalture. However, since this name has not been used for a period of time longer than 50 years, it is a *nomen oblitum* (in the sense of a decision reached, during the 1958 Zoological Congress in London) and need not be resurrected.

The Cephalic Organs of Ipnops. The surface of the head of *Ipnops* is covered by a pair of membranous bones, beneath which lie unique structures that are now known to be highly modified light-sensitive organs. Earlier theories that these structures might serve as visual rather than light-producing organs were opposed in the publication of a "Report on the structure of the peculiar organs on the head of *Ipnops*" by Moseley (*10*), for he found neither tissues which resembled the light-receptive ones of other vertebrates nor a functional optic nerve.

The organs are covered dorsally by a pair of membrane bones which are probably lateral extensions of the frontals. Beneath these bones are a pair of elongate cavities which are separated from one another. Moseley suspected that these cavities were homologous to the orbital cavities of an eyed ancestor of *Ipnops*, but this seems unlikely since the nearest known relatives of *Ipnops*, *Bathypterois* and its allies, have lateral rather than dorsal eyes. The organs themselves are membranous structures about .04 mm in thickness that cover the entire floors of the cavities.

E. Newton Harvey (*8*)[5] characterized the situation as follows:

> Finally the scopelid fish, *Ipnops murrayi* and *I. agassizi* of the Ipnopidae aroused considerable interest because of large dorsal plate-like structures on each side of the flat head. Murray and Günther had considered those of *I. murrayi*, obtained by the CHALLENGER in 1,507 fathoms, phosphorescent organs, and Moseley (1887) came to the same conclusion from a histological study. They are made up of long columnar cells with nuclei at the distal end lying above a rich plexus of blood vessels. The columnar cells are arranged in hexagonal groups separated by pigment. Branches of the trigeminal innervate the organ. Von Lendenfeld (1905), from his study of *I. agassizi*, caught by the ALBATROSS in 1,360 fathoms, also considered the structure to be a luminous disc organ, certainly not an eye, and Brauer (1908, p. 126) pointed out that the structure was quite different from that of rudimentary eyes and not supplied by the optic nerve. However, the disc is also very different from the light organs of other scopeloid fish and Rauther (1927) has held that the possibility of a peculiar photosensitive organ has not been disproved.

A suitably preserved specimen caught by the Danish GALATHEA Expedition has been intensively studied by Munk (*11*), who has shown convincingly that this structure is a light-sensitive organ similar to the usual vertebrate eye in its retinal structure and innervation but differing in the smallness of the rods and in the complete lack of a lens.

In some preserved specimens the photoreceptive tissue is yellowish and, when viewed from above, shows clearly the hexagonal outline of the vertical columns (USNM 153593, syntype of *I. agassizi*). In others (CNHM 64080, described above, and USNM 99508, a type of *I. pristibrachium*), the organ is dark purple and none of the hexagonal pattern can be seen. This difference is probably due to different methods of original preservation. In life the organs of the western Atlantic specimen described above were brilliant yellow.[6]

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[5] Citations given in this quotation are included under *Synonyms and References*, p. 154.

[6] This observation was made aboard the U.S. Fish and Wildlife Service vessel OREGON (St. 1303) by Harvey R. Bullis, Jr. (see Grey, *6*), and by the author in the Gulf of Mexico at OREGON St. 2577.

Distribution and Habitat. All species of *Ipnops* are deep-water forms known only from depths greater than 800 m. Body form and the details of capture suggest that these fishes are benthonic. *Ipnops* is now known from all major oceans, although the total number of individuals that has been captured is less than 30. Most of the known records have been summarized by Grey (5).[7]

Species. The paucity of specimens and the difficulties in interpreting the differences among the few known individuals precludes a satisfactory study of the species. There are differences in body proportions and meristic characters among all specimens and descriptions, and these differences may prove to be specific ones. Many more specimens must be caught before a fuller account of the species can be attempted. The three named forms can be separated by the *Key* that follows:

Key to Species

1a. Dorsal edge of 2nd pectoral ray[8] serrated.	*pristibrachium* (Fowler) 1943. Philippine Islands.
1b. Dorsal edge of 2nd pectoral ray[8] smooth.	
2a. Pectoral rays 15 or 16; 17 anal rays.	*agassizi* Garman 1899. Eastern Pacific.
2b. Pectoral rays 13 or 14; 13 or 14 anal rays.	*murrayi* Günther 1887, below.

Ipnops murrayi Günther 1878

Figure 42

Study Material. A single specimen, 111 mm SL, Oregon St. 1303, Gulf of Mexico off Florida, 28°47′N, 87°50′W, 1150–1200 fms., shrimp-trawl haul, May 26, 1955, CNHM 64080.[9]

Comparative extralimital material: the types of *Ipnoceps pristibrachium* Fowler, from the Philippines (USNM 99508; 99509–10); a syntype of *Ipnops agassizi* Garman from the eastern Pacific (USNM 153593); and a second Albatross specimen from off Peru (USNM 149041).

Distinctive Characters. The generic *Characters* will distinguish this species from all other fishes known from the western Atlantic.

Description. Proportional dimensions in per cent of standard length, based on the single study specimen, 111 mm.

Body: greatest depth 8.9; depth at origin of anal fin 5.9.

Caudal peduncle: least depth 3.9.

Head: length 20.0; width 10.7; depth at posterior end of light organ 6.4.

Premaxillary: length 12.8.

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[7] See p. 153 for additional Gulf of Mexico records.

[8] The first, or most dorsal, pectoral ray is a short splint which is firmly bound to the second ray.

[9] This specimen was reported by Grey (5, 6).

Dorsal fin: length of base 8.8.

Anal fin: length of base 19.3.

Caudal fin: length of middle ray 11.1; lower lobe 24.3.

Ventral fin: length 15.2.

Pectoral fin: length 14.4.

Distance from snout to origin of: dorsal fin 35.6; anal fin 67.1; ventral fin 26.6; pectoral fin 19.4; anus 31.6.

Distance from anus to: origin of anal fin 35.0; base of caudal fin 69.3; insertion of outer ray of ventral fin 6.7; nearest point on opercular flap (edge of branchiostegal membrane) 14.0; on operculum 14.9.

Scales: 53 in longitudinal series; about 6 transverse rows between dorsal and ventral midlines.

Branchiostegal rays: 10 or 11.

Gill rakers: on first arch 3 + 1 + 17.

Fin rays: dorsal 9; anal 14; caudal 1-17-1; ventral 8; pectoral 13.

Body slender, greatest depth 2.2 in hl at origin of ventral fin, where it is almost as broad as deep; ventral surface flattened anteriorly; abdomen and caudal peduncle compressed. Least depth of Caudal peduncle 5.2 in hl. Distance from snout to anus 3.2 in SL, distance from anus to root of caudal 2.4 in SL. Scales present on body and sides of head, the few scales remaining on body of study specimen large, cycloid. Fins, snout and lower surface of head naked. Lateral line single, complete and not extending onto caudal fin.

Head and Snout strongly depressed, the snout spatulate. No lateral eyes as in *Bathymicrops*. Nostrils and olfactory organs reduced, located along anterior edge of the cephalic plates. Four pores along sides of head below lateral edge of the bony cover of the luminous organ. Opercular bones membranous, not extending beyond posterior edge of branchiostegal membrane. Branchiostegal membranes extending forward nearly to tip of lower jaw, separate from one another; overlain anteriorly, near the tip of the lower jaw, by a transverse gular fold. Gill openings wide, separate from each other and from the isthmus.

Gill rakers present on all four gill arches, those of the anterior arch longer than the opposing gill filaments.

Maxillary long, expanded posteriorly, its rear third surmounted by a long and slender supramaxillary which is somewhat dilated posteriorly. Premaxillary narrow.

Teeth on premaxillary villiform and forming a band that is broader anteriorly than posteriorly. Mandibular teeth similar to those of premaxillary. Symphysis of each jaw without teeth. A narrow patch of small teeth on the rear edge of each vomerine knob. A row of minute teeth on the anterior end of the palatines.

Dorsal and Anal fins normal, their bases 11.3 and 5.2 in SL, respectively, the first dorsal ray and first four anal rays unbranched, the rest branched, the last ray of both fins split to the base; predorsal and preanal distances 2.8 and 1.5 in SL, respectively. Caudal fin long and forked, the lower lobe 0.8 in hl, the midcaudal length 1.7, the uppermost ray as well as lowermost unbranched, the rest branched. Ventral fin 1.3 in hl, the 4th and 6th rays longest, the outermost and innermost unbranched, the rest branched, the bases well separated; the fins, when expanded, lying in the same horizontal plane as the flattened interventral surface of the body; preventral distance 3.8 in SL. Pectoral fin 1.4 in hl, all rays unbranched; the prepectoral distance 5.2 in SL.

Color. In preserved specimens, body dark brown, the margin of each scale pocket colorless. Head, branchiostegal membranes, and pharyngeal and abdominal linings black. Anterior dorsal and anal rays, outer caudal and ventral rays, and pectoral fins dusky.

Size. The largest known individual is about six inches long.

Variation. I. murrayi was described by Günther from four specimens: one from the South Atlantic off Brazil, two from near Tristan da Cunha, and one from the Pacific north of the Celebes. The type locality was restricted by Grey (5) to the Tristan da Cunha locality, Challenger St. 133, about 35° S, 20°W, 3475 m; and this specimen was illustrated by Günther (7: pl. 49, fig. B). Our specimen differs in several respects from Günther's type account, but these differences are not recognized nomenclatorially here because so few data are available. The following are the more significant differences: body depth into SL 11.2 (13.5 in Günther's account); head into SL 5 (6); snout-to-anus into anus-to-caudal-base 2.19 (less than 2); preventral distance 26.6 % of SL (29.2 %, from Günther's figure); length of anal base 19.3 (15.0, from figure); and shape and extent of caudal fin, which is forked and long (rounded and shorter in figure). The significance of these differences awaits a comparison of the South Atlantic type with other specimens from throughout the western North Atlantic.

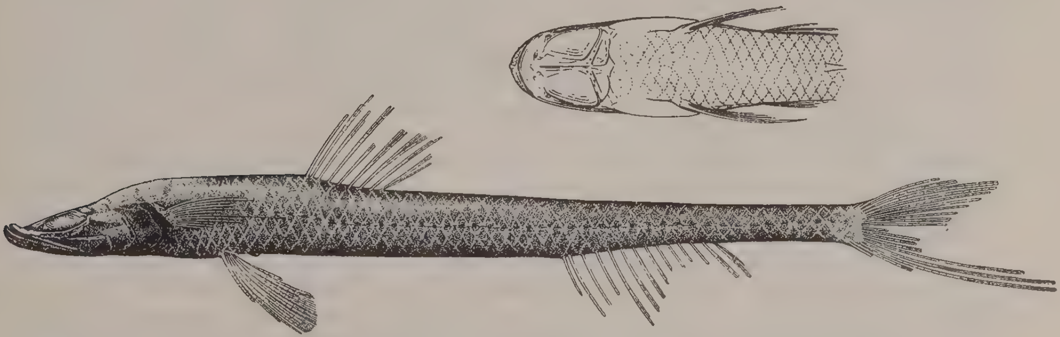

Figure 42. *Ipnops murrayi*, 111 mm long, from the northeastern Gulf of Mexico, Oregon St. 1303, 1150–1200 fms., CNHM 64080. Drawn by Margaret G. Bradbury.

Range. I. murrayi has been taken at eight Atlantic localities: off Brazil at 1600 fathoms and near Tristan da Cunha at 1900 fathoms;[10] from five localities in the Gulf of Mexico, 850–1200 fathoms;[11] and from off Bequia Island at 1507 fathoms.[12] It is also known from a depth of 800–900 fathoms off Cape Point, South Africa.[13]

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[10] Challenger St. 124 and 133.

[11] Oregon St. 1303, see *Study Material*; Blake St., 24°36′ N, 84°05′W, 955 fms.; Oregon St. 2577, 27°48′ N, 88°45′W, 850–1100 fms., July 30, 1959; Oregon St. 2820, 28°23′ N, 88°21.5′W, 1000 fms.; Oregon St. 2821, 28°47.5′ N, 87°57′W, 1000–1100 fms.

[12] Blake St. 235, "off Bequia", 1507 fms.; MCZ coll.

[13] Gilchrist (3), the specimen subsequently lost.

Synonyms and References:

Lychnoculus mirabilis Murray,[14] Manchester Sci. Lect., 9, 1877: 132 (orig. descr. popular account of the "wonderful lamp eye"; Challenger spec.).

Ipnops murrayi Günther, Ann. Mag. nat. Hist., (5) *2*, 1878: 187 (orig. descr.); Günther, Introd. to Study of Fishes, 1880: 585 (generic char.); Gill, Science, *3* (68), 1884: 620 (name only, Ipnopidae); Anon., Rep. sci. Res. 'Challenger' . . . Narrative *1* (1), 1885: 239, fig. 97 (notes on "eye"); Anon. (Murray?), Nature, July 2, 1885: 205 (fig.; in review of Narrative Voy. 'Challenger'); Günther, Rep. sci. Res. 'Challenger', Zool., *22*, 1887: 191, pl. 49, fig. B. (descr., distr.); Moseley *in* Günther, App. A, 1887: 269, pl. 67–68 (histol. structure of lum. organ); Agassiz, Bull. Mus. comp. Zool. Harvard, *15* (Three Cruises of the Blake) (2), 1888: 32, fig. 215 (fig. Blake spec., no descr. or loc.; disc. of "eyes", which he believed "destined undoubtedly to produce an image and to receive especial luminous rays."); Goode and Bean, Smithson. Contrib. Knowl., *30*, 1895: 67, pl. 18, figs. 67–68 (descr., mostly from Günther; recs. 2 Albatross spec.); Jordan and Evermann, Bull. U.S. nat. Mus., *47* (1), 1896: 547 (descr. from Günther, 1887, and Goode and Bean, 1895); Jordan and Evermann, Rep. U.S. Comm. Fish. (1895), App. 5, 1896: 298 (listed); Garman, Mem. Mus. comp. Zool. Harvard, *24*, 1899: 259, 375; pl. H, fig. 2, 2a (*cf. I. agassizi*) 400 (distr.); Boulenger, Fishes, Cambridge Nat. Hist., *7*, 1904: 613, fig. 371c (from Goode and Bean, 1895; "eyes"); Jordan, Guide to Study of Fishes, *2*, 1905: 131 (fig., cephalic discs thought to be intermediate between "true eyes and phosphorescent plates"); von Lendenfeld, Mem. Mus. comp. Zool. Harvard, *30* (2), 1905: 202 (lum. organ of *I. agassizi*, said to be same as that of *I. murrayi*); Gilchrist, Mar. Invest. S. Africa, *4*, 1908: 166 (one spec. off Cape Point, 800–900 fms. rec. only; spec. lost); Brauer, Wiss. Ergebn. 'Valdivia', *15* (2), 1908: 126 (function of "luminous" organ); Regan, Ann. Mag. nat. Hist., (8) 7, 1911: 127 (affinities with rel. inioms); Murray and Hjort, Depths of Ocean, 1912: 686 and elsewhere (gen. syst. comp.; recs., distr., luminosity, etc.); Weber and de Beaufort, Fishes Indo-Austral. Archipel., *2*, 1913: 179 (descr. and fig. from Günther); Barnard, Ann. S. African Mus., *21* (1), 1925: 231 (descr. from Gilchrist, 1906); Rauther, "Luchtorgene" *in* Bronns Klassen und Ordnung des Tierreiches, 6 (1), Bk. 2, 1927: 142, figs. 90–91 (light organ, from Moseley, 1887; Goode and Bean, 1895: Brauer, 1908); Parr, Bull. Bingham oceanogr. Coll., *3* (3), 1928: 33 (in key to bathypteroid genera); Norman, Sci. Rep. 'John Murray' Exped., *7* (1), 1939: 27 (3 spec. off Zanzibar, 1789 m; *I. agassizi* questionably distinct from *murrayi*, notes on types); Fowler, Bull. U.S. nat. Mus., *14* (2), 1943: 56 (comp. *I. murrayi* and *Ipnoceps pristibrachium*); Smith, Sea Fishes S. Africa, 1950: 117 (fig., diagn. from lit.); Harvey, Bioluminescence, 1952: 510 (lum. organ); Marshall, Aspects Deep Sea Biol., 1954: 233 and elsewhere (remarks on light organ, gen. biol.; fig.); Grey, Internat. Union Biol. Sci., (B) 16, 1954: 60 (listed); Marshall, 'Discovery' Rep., *27*, 1955: 326 and elsewhere (signif. of orientation of pectoral fin, relationships); Grey, Fieldiana: Zool., *36* (2), 1956: 136 (distr. of *I. murrayi* and rel. species); Briggs, Bull. Florida State Mus., Biol. Sci., 2 (8), 1958: 257 (listed, on the Oregon capture which forms the basis for this account); Grey, Fieldiana: Zool., *39* (16), 1958: 164 (descr., same Oregon specimen as descr. here); Munk, 'Galathea' Rep., *3*, 1959: 79–88, pls. 1–2 (histol. of eyes); Hansen and Wingstrand, 'Dana' Rep., 54, 1960: 8 (note exceptionally large erythrocytes, 19×12 μ).

Genus *Bathymicrops* Hjort and Koefoed 1912

Bathymicrops Hjort and Koefoed *in* Murray and Hjort, Depths of Ocean, 1912: 416 (and elsewhere), fig. 305; type species, by monotypy, *Bathymicrops regis* Hjort and Koefoed 1912; eastern Atlantic, about 5000 m.

Characters. Body slender. Snout depressed. Eyes minute and vestigial, covered by scales, and located far forward on the head. Scales covering head and body completely, the scales moderately large. No luminous organs. Small sharp teeth present on premaxillary, vomer and mandible. Supramaxillary absent in the single specimen seen. Gill rakers of the normal lath-like form and of moderate length, about 13 on the first arch. Color of body brownish, with darker transverse bands. Anus located near bases of ventral fins and anterior to a vertical from the origin of the dorsal fin.

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[14] See ftn. 4.

Bathymicrops regis Hjort and Koefoed 1912

Study Material. A single specimen, 95.2 mm SL, Swedish Albatross St. 342, eastern tropical Atlantic, BMNH 1949.5.5.1.

Distinctive Characters. Those of the genus.

Description. Proportional dimensions in per cent of standard length, from the single study specimen, 95.2 mm.

Body: greatest depth 7.9; greatest width 6.9.

Caudal peduncle: least depth 3.1.

Head: length 17.3; greatest width 8.4.

Eye: horizontal diameter about 0.84.

Interorbital: breadth 2.9.

Upper jaw: length 14.6.

Dorsal fin: length of base 8.0.

Anal fin: length of base 14.7.

Distance from snout to origin of: dorsal fin 43.6; anal fin 67.2; ventral fin 29.4; pectoral fin 16.4; to anus 37.6.

Lateral-line scales: about 67 (*9*).

Branchiostegal rays: about 10.

Gill rakers: on first arch 3 + 1 + 8.

Fin rays:[15] dorsal 9; anal 12; caudal I-15-I; ventral 7 or 8; pectoral 10 or 11.

Body slender, its greatest depth, immediately behind head, about 12.5 in SL, its greatest width, at origin of pectoral fin, about 1.1 in greatest body depth. Least depth of Caudal peduncle 2.6 in greatest depth of body. Anus anterior, about one third of distance from insertion of ventral fin to origin of anal fin, its distance from snout 2.7 in SL. Scales missing entirely from the available study specimen; according to Koefoed (*9*), the head and body are completely covered with scales.

Head and Snout depressed. Eyes deeply imbedded in head beneath the frontal bones and the overlying skin and scales, directed upward, and not apparent in lateral view. Gill opening very large. Opercular bones membranous. Branchiostegal membranes meeting but separate ventrally, overlapping anteriorly under the narrow transverse gular fold, and extending posteriorly but little beyond the opercular flap.

Gill rakers on first three arches lath-like, those on the last full arch reduced to spinulose protuberances; gill filaments short and apparently rudimentary, each of those on the first arches less than 0.2 of the length of the raker opposite to it.

Premaxillary long and slender. Maxillary long and flattened posteriorly in the typical fashion, not club-shaped or splint-like as in other ipnopid species; supramaxillary absent or indistinguishably fused to maxillary. Mandible turned slightly upward anteriorly.

Teeth. Symphysis of upper jaw without teeth. Premaxillary toothed throughout, the teeth minute, slightly recurved, and depressible, forming a band that is broader anteriorly than posteriorly. Mandible with teeth similar in form and arrangement to those on premaxillary. Teeth also present on palatines and vomer, those on palatine in a series, those on vomer in two patches which are not continuous with each other across the roof of the mouth.

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[15] The caudal count taken from this specimen is of interest. Although the caudal is broken and generally in poor condition, the count of I-15-I is probably correct and stands in strong contrast to the counts in all other myctophoid conditions, I-17-I, or in the Bathypteroidae, I-16-II.

Nybelin (*13*) has given the following counts for this species: dorsal—9 or 10; anal—13 or 14; ventral—8; pectoral—9 or 10.

Dorsal and Anal fins with length of base 2.2 and 1.2 in hl, the predorsal and preanal distances 2.3 and 1.5 in SL, respectively; the first dorsal ray and first two anal rays unbranched, the rest branched. Ventral fins curled toward each other, the most anterior rays of one side overlapping those of the other, the combined fins thus forming a saucer-like depression; the 1st ray unbranched, the rest branched; the preventral distance 3.4 in SL. Pectoral fins with all rays unbranched; prepectoral distance 6.1 in SL.

Color. In preservative, the single study specimen is completely colorless save for the eyes and the dark peritoneum. Koefoed (*9*), however, has provided the following color notes, which were based on less-faded material:

> The colour seems now for the most part to have disappeared, but must, as far as can be seen, have been greyish brown, darkest between the head and the ventral fins, especially on the belly. Behind the ventral fins there are dark transverse bands, one at the commencement of the anal fin, and another at its end, one between this and the caudal fin, and one at the base of the caudal itself.

Size. This species attains a length of about 111 mm.

Range. *B. regis* is known from four widely separated localities, all in the North Atlantic.[16] The depth range: 4200–5800 m. Specimens of *Bathymicrops*, not yet identified and currently under study in Copenhagen, were caught by the Galathea north of Madagascar at 4820 m, in the Indian Ocean off South Africa at 4360 m, and northeast of New Zealand at 5850 m (*4*).

References:

Bathymicrops regis[17] Hjort and Koefoed *in* Murray and Hjort, Depths of Ocean, 1912: 88 and elsewhere, fig. 305, p. 416 (orig. descr., Michael Sars St. 48: 28°54′N, 24°14′W, about 5000 m; comp. eyes with related species); Koefoed, Rep. 'Michael Sars' N. Atlantic Deep-Sea Exped., *4* (1), 1927: 64, pl. 5, figs. 1–3 (descr.); Parr, Bull. Bingham oceanogr. Coll., *3* (3), 1928: 23 (in key, diagn.); Fowler, Bull. Amer. Mus. nat. Hist., *70* (1), 1936: 347 (after Murray and Hjort, 1912; listed); Harvey, Bioluminescence, 1952: 552 (mentioned, with *Ipnops*, as totally blind); Bruun, Internat. Union Biol. Sci., (B) 16, 1954: 86 (part, noted as an example of a deep-sea species with a restricted bathymetric range, 4200–5800 m); Nybelin, Internat. Union Biol. Sci., (B) 16, 1954: 70 (Swedish Albatross spec. listed); Marshall, Aspects Deep Sea Biol., 1954: 232, pl. 9 (eyes *cf. Ipnops*); Marshall, 'Discovery' Rep., 27, 1955: 326 (position and signif. of angle of insertion of pectoral fin, relationships); Grey, Fieldiana: Zool., *36* (2), 1956: 135 (distr., refs.); Nybelin, Rep. Swedish Deep-Sea Exped., *2* (Zool.), *20*, 1957: 257 (descr., two e. Atl. recs. and one from w. N. Atl. S. of Grand Bank off Newfoundland; Swedish Albatross Sts.).

Doubtful References:[18]

Bathymicrops regis, Bruun, Internat. Union Biol. Sci., (B) 16, 1954: 86 (distr., Pac. and Indian O. spec. probably not *B. regis*); Grey, Fieldiana: Zool., *36* (2), 1956: 92 (from Bruun, Proc. Eighth Pacific sci. Congress,

[16] Michael Sars St. 48, 28°54′N, 24°12′W, about 5000 m; Swedish Albatross St. 313, haul 1, 29°48′N, 17°39W to 30°05′N, 17°18′W, 4267–4255 m; St. 342, haul 4, 01°03′N, 18°40′W to 00°58′N, 18°37′W, 5250–5300 m; St. 363, haul 8, 12°22′N, 52°00′W to 12°13′N, 51°44′W, 5044–5033 m.

[17] Frequently misspelled *regius*.

[18] If the figure given by Bruun (*2*) is typical of the Pacific form and of that provided by Hjort and Koefoed in their original account of 1912 of the Atlantic population, the two probably represent different species.

apparent preprint 1955; gives GALATHEA locs. as follows: "north of Madagascar, 4820 meters; Indian Ocean off South Africa, 4360 meters; northeast of New Zealand, 5850 meters."); Bruun *in* Mem. geol. Soc. America, *67* (1), 1957: 665 (part, distr.); Bruun, Proc. Eighth Pacific sci. Congress, *3* (Oceanography), 1958 (1957): 367, 371 (fig., distr.; given as example of a cosmopol. abyssal sp.; name misspelled *Bathymictops regius*).

Genus *Bathytyphlops* Nybelin 1957

Bathytyphlops Nybelin, Rep. Swedish Deep-Sea Exped. 1947–1948, *2* (Zool.), 3, 1957: 258; type species, by original designation, *Bathymicrops sewelli* Norman, Sci. Rep. 'John Murray' Exped. 1933–34, *7* (1), 1939: 26; Arabian Sea, 3840 to 3872 m.

Characters. Eyes very small and covered by skin. Gill raker at angle of arch much enlarged and strong, the others reduced to dentigerous ossifications that do not project above the gill arch. Patches of minute granular teeth present on jaws, vomer, palatines, pterygoid and pharyngeals. Pectoral rays 11–13. Dorsal rays 11–14. Ventral rays 8. Maxillary horizontally flattened throughout most of its length; vertically compressed posteriorly. Supramaxillary small. Body slightly compressed and relatively deep, its depth about 6 in SL. Caudal fin forked. Background color light, the scale pockets edged with black; sides of head and fins black.

Range. The species of *Bathytyphlops* are known from deep water of the Arabian Sea (*B. sewelli*; 3840 to 3872 m), from the Straits of Florida north of Cuba, and from unspecified localities along the course of the Danish GALATHEA Expedition (*1*).

Bathytyphlops marionae Mead 1959

Figure 43

Study Material. Two specimens: the type, 279.0 mm SL, OREGON St. 1955, Caribbean off Honduras, 16°48′N, 82°33′W, 550 fms., Sept. 17, 1957, CNHM 64439; 1, 263.0 mm (paratype), ATLANTIS St. 2991, Strait of Florida north of Cuba (Harvard-Havana Exped.), 23°21′N, 80°23′W, 475 fms., March 14, 1938, MCZ 39394.

Distinctive Characters. B. marionae can be distinguished from its single congener, the Arabian Sea *B. sewelli* (Norman), by the following characters: eyes minute but pigmented and with well-developed lenses, covered by skin but not by scales; pectoral fin 12 or 13; dorsal 12 or 13; anal 13 or 14; lateral-line scales 64 or 65 (in the Indian Ocean *B. sewelli*: pectoral 11, dorsal 11, anal 16, scales 60).

Description. Proportional dimensions in per cent of standard length, of the type, 279.0 mm, followed by those of the 263.0-mm paratype.

Body: depth 16.0, —; depth at origin of anal fin 10.3, 9.9; greatest width 9.4, 9.8.

Caudal peduncle: least depth 7.7, 7.2.

Head: length 23.1, 22.4.

Snout: length 7.5, 6.6.

Eye: horizontal diameter 0.7, 0.8.

Interorbital: width 8.6, 8.5.

Premaxillary: length 17.0, 16.6.

Dorsal fin: length of base 12.7, 12.2; depressed height 21.7, 20.1.

Anal fin: length of base 14.0, 12.4; depressed height 19.4, 17.2.

Caudal fin: length of central ray 8.6, 10.4.

Ventral fin: length 16.7, 15.4.

Pectoral fin: length 20.1, 17.1.

Distance from snout to origin of: dorsal fin 39.1, 40.3; anal fin 69.6, 69.0; ventral fin 37.5, 37.9; pectoral fin 21.3, 21.7.

Distance from: insertion of ventral fin to origin of anal fin 32.4, 33.2; end of base of dorsal fin to end of midcaudal ray 47.5, 48.3; end of anal base to base of midcaudal ray 17.6, 17.5; anus to origin of anal fin 22.0, —; anus to insertion of ventral fin 10.8, —.

Scales: lateral line 64 or 65; from dorsal to lateral line 8; from lateral line to anal 6.

Branchiostegal rays: 15–17.

Fin rays: dorsal 12 or 13; anal 13 or 14; caudal 1-17-1; ventral 8; pectoral 12 or 13.

Vertebrae: 63 or 64 including urostyle.

Body moderately compressed, snout somewhat depressed, the body deepest at origin of dorsal fin, this depth about 1.4 in hl, about 6.2 in SL; depth at anal origin 2.2–2.3 in head; greatest width about 1.7 in greatest depth. Least depth of Caudal peduncle 3.0–3.1 in head. Anus about a third of the distance from insertion of ventral fin to origin of anal. Scales present on entire top of head, cheeks, anterior part of branchiostegal membrane, isthmus and gular membrane, entire body, and base of caudal rays; the scales (as well as can be determined) cycloid, deciduous (few scales remain on the two study specimens); a broad sheath of scales extending across venter between and partly covering bases of inner ventral rays; an enlarged rounded scale in axil of pectoral fin, and rows of more elongate scales along bases of dorsal and anal fins. Lateral line well developed, the scales pierced by a longitudinal tube that also opens above and below; lateral line begins above base of pectoral fin and ends at base of caudal, not continuing onto caudal fin.

Head of moderate size; lower jaw terminal; the head about a fifth of SL, 4.3–4.5 in SL; its rear margin formed by the branchiostegal membrane, its rear border (edge of gill cover) sloping obliquely downward and backward, the most posterior point below the posterior half of the base of the pectoral fin. Top of head covered by skin and scales; the head bones well ossified. Eye minute, covered by skin but apparently not scaled over. A few poorly ossified Circumorbital bones floating free in skin around eye. Interorbital width 2.6–2.7 in hl. Olfactory organs well developed, slightly closer to tip of snout than to eye; a thin tube around anterior nostril, enlarged into a flap posteriorly between the nostrils. Behind each posterior nostril is a pair of slits that do not communicate with the olfactory cavity; their function is not apparent. Top of head with fewer ossified pores than in most related species. Opercular bones large and well ossified, the operculum ending posteriorly with the well-developed suboperculum. BRANCHIOSTEGAL MEMBRANES broad, free from the broad, scaled isthmus and from each other, the left overlapping the right, the membranes scaled, covered anteriorly by a thick, broad, and scaled transverse gular fold. BRANCHIOSTEGAL RAYS well developed, the uppermost not much flattened.

GILL RAKERS on first arch consist of one large heavy raker at the angle and of basal ossifications that probably represent rudiments of rakers. The length of raker at angle is equal to the distance between nostrils. About 6 basal ossifications on the epibranchial, 12–14 on the ceratobranchial; these rudiments, the edges of the branchial bones, and the enlarged raker at the angle are covered by minute, short spines that provide a rugose surface similar to the tooth patches on jaws and vomer. The succeeding arches bear similar rugose patches, and the pharyngeals are completely covered with patches of similar but larger teeth.

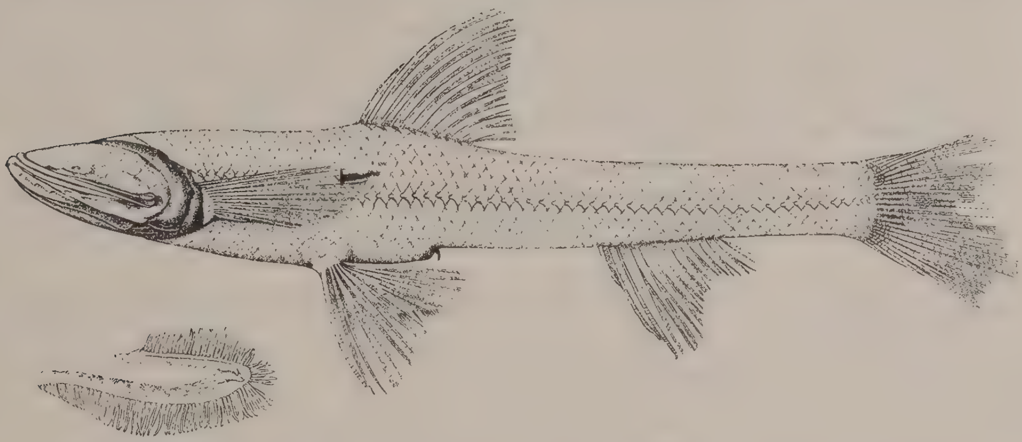

FIGURE 43. *Bathytyphlops marionae,* 279 mm long, from the Caribbean off Nicaragua, OREGON St. 1955, 550 fms., and the left anterior gill arch of the same individual, CNHM 64439. Drawn by Mildred H. Carrington.

PREMAXILLARY long and slender, 1.3–1.4 in hl, the lower and outer surface completely covered with denticles, giving the bone a rugose appearance. MAXILLARY, for most of its length, slender when viewed from the side, but expanded in the horizontal plane. Posteriorly, it is expanded vertically and surmounted by an irregularly shaped supramaxillary. A short fleshy flap at posterior end of maxillary. MANDIBLE broad and heavy, its outer lower surface pierced by the series of pores characteristic of many deep-water iniomous fishes; its lower edges well separated from each other (in contrast to the situation in the bathypteroids, in which the lower edges of the dentaries very nearly meet along the midventral line). Mandible ending anteriorly in a small knob. Articular bone exceptionally long, extending forward half the distance from joint of mandible to tip of lower jaw.

TEETH on palatine, pterygoid, and vomer similar, the toothed patches large, the two patches on vomer separated by a deep trough. No teeth at symphysis of either jaw.

DORSAL fin inserted close behind a vertical from insertion of ventral; predorsal distance 2.5–2.6 in SL; the first 2 rays simple, the rest branched, the last ray branched to its base; distance from origin to tip of fin when depressed, 4.6–5.0 in SL; the length of its base about 1.8 in hl. ANAL fin placed posteriorly, the preanal distance 1.4–1.7 in SL; the distance between the end of its base and the base of midcaudal ray about 5.7 in SL; height of fin (depressed) 1.2–1.3 in hl; 2 or 3 rays simple, the remainder branched. CAUDAL fin forked, the lobes equal. VENTRAL fin with only the outer ray unbranched; its length 1.4–1.5 in hl, preventral distance 2.6–2.7 in SL. PECTORAL fin extending to base of ventral fin, its length 1.1–1.3 in hl; the prepectoral distance 4.6–4.7 in SL, the 2 uppermost and 2 lowermost rays simple.

Color. In alcohol, pale with dark edges around the scale pockets. Head dark. Branchiostegal membrane, fins, and linings of body cavities black.

The body color may be wholly dark when the animal is alive and has its skin and scales intact.

Range. B. marionae is known only from the two specimens referred to under *Study Material* above, and a third from deeper water in the central Gulf of Mexico.[19]

Reference:

Bathyphlops marionae Mead, J. Wash. Acad. Sci., *48*, 1959: 370, fig. 4 (orig. descr., from same two specimens discussed above).

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[19] OREGON St. 2574, 26°34′N, 89°53′W, 1450 fms., July 28, 1959.

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COLLECTING FROM NAVIGATION BUOYS

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Buoys are placed by necessity at navigational vantage points along practically all coastal and large inland waterways. When they are brought in for periodic cleaning and servicing by the Coast Guard, many attached or clinging species of marine life are available for study. Close observation of the community structure, systematic sampling of the marine life, and diligent recording of the findings uncovers a wealth of scientific information often otherwise unobtainable. Research along this line offers unusual opportunities for study, some of which are discussed below.

The dominant species in a fouling community usually changes at different latitudes along the coastline. Also the geographical limits of many species can be established by examination of buoys along the coast. This is of considerable interest not only to the zoogeographer but to governmental and private agencies whose vessels and marine installations are subject to fouling by these species. By serving as test surfaces for new types of anti-fouling paints, navigational buoys are a useful research adjunct.

If the investigator is able to spend some time aboard the buoy tenders he will be rewarded with many interesting observations denied to one who only examines buoys after they have been brought ashore. He can observe first-hand the ecological aspects of the living species. Fortunately, however, most buoy species are attached and usually still alive when a buoy is brought ashore. Many basic observations can therefore be made ashore as well as at sea.

After preliminary observations the buoys can be sampled according to the interests of the investigator. For quantitative studies, I restrict my collecting to the contents of a square foot of surface from a particular area on each buoy. For species studies I sometimes collect large numbers of individuals from several buoys. Another person might plan an experiment around an accessible species available through periodic removal from buoys. I have found that enough buoys are brought in each year to set up planned experiments involving the more common species from an area. And because live individuals of most attached forms can generally be obtained, anatomical or histological studies are practical.

When the buoy chain and mooring are available even the vertical distribution of certain species of fouling organisms can be studied. As the winch of a Coast Guard vessel reels in lengths of chain, the transition from an abundance of fouling organisms to no growth at all is often clearly evident.

Since buoys are surface vehicles, they also serve as "spat collectors," and species with true pelagic larvae are apt to settle on them. Settling habits and the mechanics of attachment in early postlarval forms can be observed and studied.

Buoys are on station for known lengths of time, usualy one to two years, although some may be out for only a few weeks or months. Thus, when numerous buoys from an area have been examined, definite spawning season limits can be prescribed for some species. Length-frequency data collected at the same time will affix modal strengths and provide minimum growth rates for these species. Buoys out for a short length of time can contribute very important information—especially towards establishing the length of the spawning season, and for estimating seasonal growth rates.

Questions pertaining to speciation may also be answered by careful study of buoy material. Investigators are frequently handicapped by the lack of a series of specimens sufficient to show the extent of natural variation in a species. As many thousands of a single species are often available from a buoy, variance within a population can easily be studied. Studies of variation in such populations are of special interest since ecological factors are similar for all individuals, i.e., the microhabitat on the buoy is more equable than the usual habitat on the bottom. Thus variation can be more clearly defined as genetic rather than ecotypic. At the same time changes in gross morphology can be ascertained, especially those great changes that occur in the immediate postlarval to juvenile stages of ontogeny.

Species that normally settle and live in deep water, but that do settle and survive on buoys subject to greater surface temperature variation, can be assigned temperature tolerances. Determination of mortality rates may also be attempted by the analyst. Ecologists might be more interested in studying community organization, community succession, or the orientation and adaptation of species.

The spawning grounds, the length of the larval period, the direction and rate of speed of water currents—these and other indirect issues can be given at least philosophical consideration as more and more information becomes available through such studies.

With all the opportunities afforded by this type of study it is very surprising to find so little published work on the subject. Each buoy has its own complex community structure—a totality of related parts. Contribution resulting from planned marine research using this harvest cannot help but further the progress towards a better understanding of some of the biological intricacies involved.

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SHELL REPAIR IN THE SEA SCALLOP, *PLACOPECTEN MAGELLANICUS*

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(Abstract)

The sequence of repair of both the internal and peripheral shell of sea

scallops was observed during laboratory experiments as part of a study to determine mortality due to shell breakage from repeated dredging in areas of high scallop concentrations. After shells of living animals were cracked, or broken, or the edges chipped, the animals were sacrificed periodically and shell repairs or partial repairs examined. In every scallop the mantle first exuded a noncalcareous layer, a film of conchiolin, over the site of shell injury. Deposition of shell material then proceeded—first with the formation of calcium droplets over the organic substance, then with the secretion of shell material about the droplets to fill in the area. After this initial process had been accomplished, successive layering gradually thickened the shell in the repair area.

The inorganic chemical composition of the scallop shell is calcitic except for a minor percentage of aragonite secreted in the muscle-attachment areas. Repair of shell damage through the region of the insertion of the adductor muscle proceeded as described for repairs through regions of mantle tissue.

Major shell damage produced greater mantle activity that formed greater quantities of conchiolin and molded the damaged area close to the original, structurally sound, shape. When damage was major, the frequent fracture of the thin crusts of new shell material necessitated repeated repairs before the entire process was complete.

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BENTHIC ECOLOGY AND FAUNAL CHANGE RELATING TO OYSTERS FROM A DEEP BASIN IN THE LOWER PATUXENT RIVER, MARYLAND

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ABSTRACT

Living oysters from deep water (130 feet) were taken in an area of the lower Patuxent River. These oysters were studied to determine their well-being at this unusual depth. This was done by comparing the benthic ecology, including faunal changes, physical and chemical parameters and oyster growth rate at the deep-water station with shallower water stations nearby. Faunal change was more variable at the deep-water station, but physical and chemical characteristics were similar at all stations. The oysters from 130 feet grew more slowly; however, they were successful in maintaining a population and surviving well under rather unusual conditions.

INTRODUCTION

The main distribution and abundance of the American oyster, *Crassostrea virginica* (Gmelin), is in shallow estuarine waters. Galtsoff (1964) gave 100 feet as the greatest depth in which *C. virginica* lives. Merrill, Emery, and Rubin (1965), from scattered data relative to present bathymetric distribution of natural oyster populations in Chesapeake Bay, estimated 6 meters (about 18 feet) as the average depth.

Since oysters usually live in shallow water, the following observation in a Report by the Board of Shellfish Commissioners of Maryland (1912, p. 120) of living oysters at an unusually great depth in an area of the lower Patuxent River, Maryland, is of interest and significance:

> In the vicinity of Point Patience, oysters were taken at depths of 120 and 130 feet, and the results of the examination in this deep water showed the bottom to be densely stocked and the oysters to be in a most thriving condition. While the oysters may originally have been carried to these deep bottoms from adjoining oyster bars by currents (as many oyster men claim), no evidence was found to indicate that the conditions of the deep lying bottoms are not just as favorable for the growth of oysters as those which prevail on the bottoms in shallower water.

Stimulated by the Maryland Report, we investigated the current status of the oyster population in this deep basin. Upon confirmation of the existence of the oysters in depths of 130 feet off Point Patience (Boss and Merrill, 1965), we felt that a comparison of this population with populations from shallower depths in the same area would be valuable. Therefore, at several stations in June and December 1964, chemical and physical data were taken, growth rates of shells of the oyster and "condition" indices of the oyster meats were determined, and changes in faunal composition recorded. This paper reports the results of the study.

DESCRIPTION OF THE AREA

The inset in Figure 1 shows the geographic position of the Patuxent River as it enters the western part of Chesapeake Bay at Solomons, Maryland, about 25 miles north of the mouth of the Potomac River. The Patuxent River is approximately 80 miles long and drains an area of about 960 square miles (Bonsteel and Burke, 1907). The lower por-

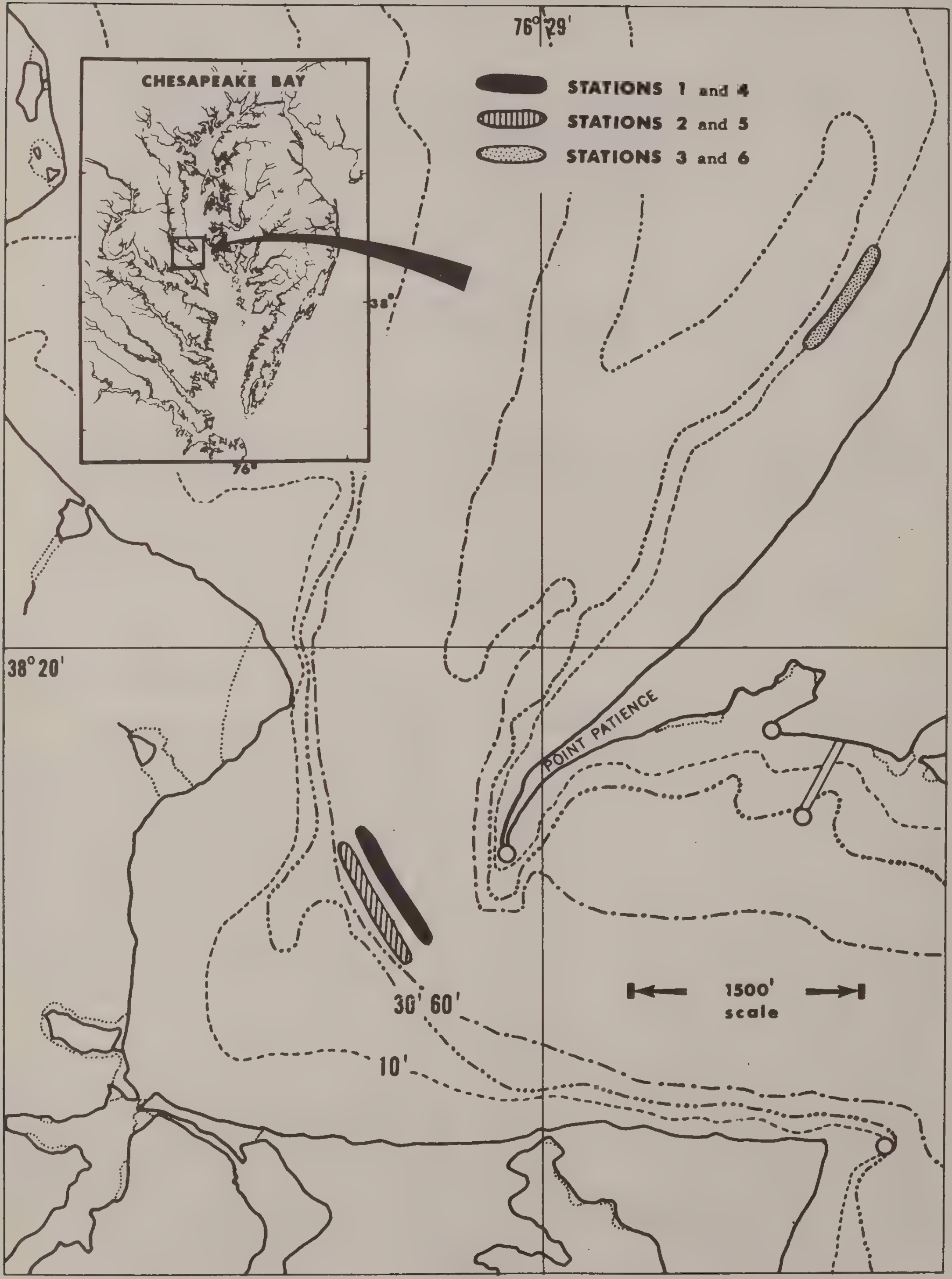
76°29'
CHESAPEAKE BAY
STATIONS 1 and 4
STATIONS 2 and 5
STATIONS 3 and 6
38°
76°
38°20'
POINT PATIENCE
30'
60'
10'
1500' scale

TABLE 1. *Plotted positions of dredging stations in the lower Patuxent River. Stations 1-3 (June); repeat Stations 4-6 (December). Locations are taken from Coast and Geodetic Survey Chart 553.*

Station	Date	Lat. (N)	Long. (W)	Depth (Feet)
1	12 June 1964	38°19′44″	76°29′15″	130
2	12 June 1964	38°19′41″	76°29′18″	65
3	12 June 1964	38°20′30″	76°28′27″	10
4	3 Dec. 1964	38°19′44″	76°29′15″	130
5	3 Dec. 1964	38°19′41″	76°29′18″	65
6	3 Dec. 1964	38°20′30″	76°28′27″	10

tion of the river is estuarine and has a tidal amplitude of 1.4 feet at the mouth of the estuary and 2.9 feet near its upper limit (Nash, 1947).

Stations were established off Point Patience at positions and depths indicated in Table 1 and Figure 1. The area sampled is about 1 mile upstream from Solomons in tidal zone V as classed ecologically by Mansueti (1961). This portion of the river has a steeply walled channel or basin which at places exceeds a depth of 130 feet. Pritchard (1951) noted that the lower Patuxent River has a subsurface upstream movement of saline water and a surface downstream current of fresh water with each tidal cycle.

Station positions were established on board ship by triangular alignment with salient land features and depth readings on the fathometer. As in the study by McErlean (1964), the exact positions are subject to some degree of error, in the range of 30 feet.

PHYSICAL AND CHEMICAL CHARACTERISTICS OF THE AREA

Physical and chemical data were taken at each station at the surface and bottom. The salinity and temperature were recorded simultaneously with a salinometer. Oxygen determinations were made by the Winkler method and chlorophyll "a" measurements by spectrophotometric analysis. Table 2 summarizes these measurements.

Temperatures in June were nearly isothermal (22.1-22.4°C), except for the bottom temperature at the deep-water station which was 21.0°C. Likewise, water temperatures were closely similar in December (8.0-8.7°C); the shallow-water surface waters were slightly cooler than the bottom waters.

Salinities in June were also similar (11.29-12.23 ppt), but the bottom waters were slightly more saline (by less than 1 ppt). The situation was the same in December, when salinity averaged 18.5 ppt.

Oxygen levels were low at all stations in June. Values ranged from 7.46 to 7.99 ppm except at the bottom at the deep-water station where the concentration was 5.99 ppm. Oxygen values were higher in December; they averaged about 11 ppm but were somewhat lower at all bottom stations and lowest at the deep-water station (10.66 ppm). These levels indicate fair circulation the year around.

Chlorophyll "a" was generally low at all stations in both June and December. In each season, however, the amount was lowest on the bottom at the deep-water station.

FIG. 1. *Geographic location of the lower Patuxent River in the area of Pt. Patience (inset) and location of stations at which oysters were collected. The 10-, 30- and 40-foot depth contours are shown by broken lines.*

"CONDITION" OF OYSTERS

A "condition" index was established for the summer samples by visual examination of the oyster meats, and for the winter samples by determination of the percentage dry weights of the meats (Table 3). Each sample contained 10 adult oysters. The condition of the oysters in shallow water was better in both seasons than in either the deep or medium water. No samples contained oysters that would classify higher than average and no oysters would classify as good.

GAMETOGENESIS OF OYSTERS

Sex of 10 oysters from each station in June and December was determined and the conditions of the gonads recorded. In June, oysters from all stations appeared ready to spawn (gonads classified as "ripe"). In December, gonads of the oysters from shallow depths were flaccid, but some of those from deep and medium-deep stations were only partially spawned. At the medium-deep station the gonads of 3 of the 10 oysters contained some eggs or sperm; at the deep-water station, 4 of the 10 had only partially spawned. The sexual products were still viable. Fertilization took place when eggs and sperm were placed together in the laboratory. Larvae developed through to the "straight-hinge" veliger stage.

TABLE 2. *Physical and chemical data at dredging stations in the lower Patuxent River. Stations 1-3 occupied June 12, 1964; stations 4-6, December 3, 1964.*

Station	Depth (feet)	Temperature (°C)		Salinity (ppt)		Oxygen (ppm)		Chlorophyll "a" (μg/l)	
		Surface	Bottom	Surface	Bottom	Surface	Bottom	Surface	Bottom
1	130	22.10	21.00	11.67	12.23	7.92	5.99	1.38	1.17
2	65	22.40	22.30	11.29	11.73	7.96	7.46	1.62	1.42
3	10	22.30	22.30	11.38	11.46	7.99	7.96	1.78	2.70
4	130	8.42	8.68	18.46	18.92	11.51	10.66	3.34	1.87
5	65	8.42	8.55	18.57	18.67	11.25	10.90	2.35	4.31
6	10	8.00	8.49	18.20	18.57	11.26	10.71	2.17	2.07

To our best knowledge, these populations of oysters are the only natural oysters in the Chesapeake area that could be utilized out of season for spawning experiments.

THE BENTHIC FAUNA AND CHANGES IN THE FAUNAL COMPOSITION

A 5-minute tow was made at each station with a standard 30-inch oyster dredge with a 3-inch-mesh bag. At no station was the bag completely filled. Biological materials were sorted after each tow and all, or an aliquot, of the material was preserved. Table 4 lists the various species of animals found at each station and their abundance. The data for the stations show a seasonal fluctuation in the population of certain species.

The most noticeable changes in the faunal composition were at deep-water stations 1 and 4. Both the oysters, *Crassostrea virginica*, and the mussels, *Brachidontes recurvus*, showed a nearly 10-fold decline in numbers in the December dredging as compared with the June dredging. The numbers of the sea grape, *Molgula manhattensis*, increased sharply in December and the anemone, *Aiptasia eruptaurantia*, declined. Both *Molgula* and *Aiptasia* are sedentary organisms which often attach to the shells of oysters or mussels.

The increase in *Molgula* in deep water was phenomenal — from 200 per 5-minute tow in June to an estimated 30,000 in December. Of the 2-bushel volume of material in the deep-water dredge haul in December, *Molgula* made up about 1 1/2 bushels.

The dominant epizoic organism of the oyster at the medium-depth station in December was the red-finger sponge, *Microciona prolifera*. This species fouled oyster shells heavily, but did not appear to affect the oyster population adversely. Although the sponge was dominant, it was highly localized; it was found only in December and only at this station.

GROWTH OF OYSTERS AND MUSSELS

Shapes of the oysters ranged from long and narrow to ovate. To obtain a comparable shell size for all shapes, measurements of height and length of the oysters were taken, totalled, and the sum divided by 2. After size frequencies were established an attempt was made to separate the populations into age groups with the aid of probability paper as described by Harding (1949). This separation was not possible because the great variation in yearly growth masked the modes of the age groups. The mode of first-year oysters was easily distinguished, however, in all collections. A mean, calculated to represent that group, provided an index of growth for the first-year oysters at each station. This figure is the "low" mean in Table 5. The remaining oysters in each collection were given a "high" mean which represents the remaining range of ages.

Each oyster population showed growth during the 7 months as indicated in both "low" and "high" means in Table 5. The mean size of the small oysters in deep water was less than at the other stations on both collecting dates. Furthermore, the mean growth for the juveniles of the deep-water population was less, only 11 mm in 7 months com-

TABLE 3. *"Condition" of Oyster Meats.*

Stations	Depths (feet)	12 June 1964 (by observation)	2 December 1964 (by percentage solids)
1 and 4	130	Medium minus	10.20
2 and 5	65	Medium	9.81
3 and 6	10	Medium plus	12.77

TABLE 4. *Benthic fauna, in numbers of individuals per 5-minute tow, taken at stations off Point Patience in the lower Patuxent River, Maryland (Stations 1-3, June 1964; Stations 4-6, December 1964).*

	Station numbers, and depths in feet (in parenthesis)					
	1	2	3	4	5	6
Organism	(130)	(65)	(10)	(130)	(65)	(10)
Porifera						
Microciona prolifera (Ellis & Solander)	—	—	—	—	abundant	—
Coelenterata						
Aiptasia eruptaurantia (Field)	400	—	—	52	308	—
Aiptasiomorpha luciae (Verrill)	—	—	—	—	4	—
Diadumene leucolena (Verrill)	—	—	2	—	—	66
Thuiaria argentea (Linnaeus)	—	—	—	some	—	—
Annelida						
Nereis (Neanthes) succinea (Frey & Leuckart)	—	5	54	32	114	122
Polydora ligni Webster	—	1	1	—	—	—
Phyllodoce (Anaitides) maculata (Linnaeus)	—	—	—	6	11	—
Glycera dibranchiata Ehlers	—	—	—	2	—	—
Polyclad worms	—	—	—	—	3	3
Crustacea						
Balanus improvisus Darwin	many	many	—	—	common	common
Balanus eburneus (Gould)	common	common	—	—	rare	rare
Callinectes sapidus Rathbun	—	—	4	—	—	—
Eurypanopeus depressus (Smith)	8	101	1	23	66	52
Rithropanopeus harrisii (Gould)	36	12	—	12	2	—
Crangon septemspinosus (Say)	2	—	—	7	—	—
Palaemonetes pugio Holthuis	—	6	—	—	—	—
Palaemonetes vulgaris (Say)	—	—	—	1	10	—
Palaemonetes intermedius Holthuis	—	—	—	—	6	—
Mollusca						
Nassarius vibex (Say)	6	—	1	18	—	—
Epitonium rupicola (Kurtz)	16	—	—	2	—	—
Odostomia impressa (Say)	—	—	2	—	—	—
Odostomia bisuturalis (Say)	—	—	—	—	4	—
Haminoea solitaria (Say)	—	—	34	—	—	—
Crassostrea virginica (Gmelin)	258	1677	227	49	1058	162
Brachidontes recurvus (Rafinesque)	1004	1356	47	51	546	62
Mulinia lateralis (Say)	—	—	—	—	—	5
Gemma gemma (Totten)	—	—	12	—	—	—
Mya arenaria (Linnaeus)	3	18	4	—	—	—
Tagelus plebius (Solander)	—	—	41	—	—	—
Macoma balthica (Linnaeus)	5	8	1	—	—	1
Laevicardium mortoni (Conrad)	—	1	—	—	—	—
Tunicata						
Molgula manhattensis (DeKay)	200	120	5	30,000	648	293
Pisces						
Gobiosoma bosci (Lacepede)	—	6	4	3	2	1
Gobiesox strumosus Cope	—	—	2	1	2	—
Chasmodes bosquianus (Lacepede)	—	—	1	1	6	1
Opsanus tau (Linnaeus)	—	—	3	3	2	—
Syngnathus fuscus Storer	—	—	—	3	2	—

TABLE 5. *Comparison of oyster populations per 5-minute tow at three depths in the lower Patuxent River, Maryland in the summer and winter of 1964. Stations 1-3 sampled June 12, 1964; stations 4-6, December 3, 1964. (See text for explanation of low and high means.)*

Station	Depth (feet)	Number in Sample	Low Mean (mm)	High Mean (mm)
1	130	258	22	67
2	65	1677	27	69
3	10	227	25	93
4	130	49	33	69
5	65	1058	43	76
6	10	162	47	97

TABLE 6. *Size range (10-mm intervals), and average sizes of a sample of* Brachidontes recurvus *from Stations 1-6, lower Patuxent River.*

Size	Stations					
(mm)	1	2	3	4	5	6
1-10	7	13	1	3	7	2
11-20	78	44	8	14	28	12
21-30	146	50	12	17	41	14
31-40	182	71	13	13	96	15
41-50	83	44	10	3	82	11
51-60	11	4	2	1	17	8
61-70	—	—	1	—	1	—
Total	502	226	47	51	273	62
Average	31	30	30	27	35	33

pared with 16 mm at the 65-foot station and 22 mm at the 10-foot station. The change through 7 months in the "high" mean reveals a similar situation in that the growth for the entire population of the oysters at the deep station was lower.

While the oysters from 130 feet grew more slowly than those at either of the shallower stations, they were maintaining a population and surviving well under rather unusual conditions.

Although the oysters from deep water, as a population, exhibited growth for the period of study, the population of mussels showed "negative" growth. An attempt to separate the modes for age groups of the mussel, *Brachidontes recurvus*, was unsuccessful. In every collection the total size frequency of the population blended into an indistinguishable single mode (Table 6). The lack of a distinctive "low" mean can be explained by the long spawning season of *B. recurvus*. Allen (1962) and Shaw (1965) have shown that this mussel spawns over a long period, possibly from April to December. An almost continual setting of post-larvae during the growing season would make it impossible to establish a mean for young-of-the-year.

The mean size for mussels increased at the medium-deep and shallow-water stations over the 7 months, but decreased sharply at the deep-water station. The decrease of size at the deep-water station is attributable to the lower ratio of larger to smaller animals (Table 6, compare stations 1 and 4). Greater mortality of larger mussels would account for the decrease in mean size.

Molgula and *Brachidontes* are of a similar size and both foul the oyster, which is much larger. *Molgula*, like the oyster and mussel, is an extremely efficient suspension feeder, and has a surprisingly high dry-weight of about 5 per cent (Haven [1], in litt.). Galtsoff (1964) found that oysters suspended on rafts off Cape Cod, Massachusetts, showed no ill effects when they were totally covered with fouling organisms, including *Molgula*. The great numerical increase of *Molgula*, however, may have adversely affected the growth of mussels through direct competition.

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[1] Dexter Haven, Virginia Institute of Marine Science, Gloucester Point, Virginia.

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FURTHER NOTE ON DISTRIBUTION OF CYMATIIDAE IN WESTERN ATLANTIC. — Range extensions for juveniles of two species of Cymatiidae found on navigation buoys off South Carolina were reported by Merrill (1961, Nautilus *75* (3) : 94-95). He postulated that the specimens were adventitious, that in their larval stage they had been carried northward of their normal range by the Gulf Stream, and therefore probably were unable to overwinter and reproduce at the higher latitude. This supposition was strengthened by the fact that no Cymatiidae had been reported from bottom habitats north of southern Florida in the latest monograph (Clench and Turner, 1957, Johnsonia 3 (30) : 189-244).

The occurrence of larval cymatiids in the Gulf Stream north of their reported range can now be documented. Dr. Rudolph Scheltema of the Woods Hole Oceanographic Institution has been collecting plankton extensively in the open waters of the Atlantic Ocean. He informs us (personal communication) that larval Cymatiidae are widely distributed in his collections over the North Atlantic. One species, probably *Cymatium parthenopeum*, was taken from a sample east of the Grand Banks at Latitude 47°30′, much farther north than adults are recorded.

Mr. Richard Petit of Ocean Drive Beach, South Carolina brought to the attention of the senior author the fact that a shrimp trawler had dredged a live specimen of *Cymatium parthenopeum*, 93 mm. long, 40 miles offshore of McClellanville, South Carolina, in 40 fathoms, June 1962. This find stimulated extensive dredging by Merrill and Petit in the offshore waters of South Carolina. The work produced many new range extensions, most of which were several hundred miles northward from southern Florida. The first report of these extensions has been published (Merrill and Petit, Nautilus *79* (2) : 58-66) . In all, 5 species of *Cymatium* now have been reported from South Carolina.

Two species of *Cymatium* were later taken from the catch made by a trawler in January 1963, southeast of Cape Lookout, North Carolina, in 18-20 fathoms. Two specimens of *Cymatium parthenopeum* (Von Salis) 1793 measured 95 and 195 mm. (I.F.R., U.N.C. Moll. Coll. #1107.1 and 1107.2) and two specimens of *Cymatium poulsenii* (Mörch) measured 65 and 72 mm. (I.F.R., U.N.C. Moll. Coll. #1106.2 and 1106.1) . The collections at Cape Lookout extended the known range of both species, which have been reported previously from South Carolina by Merrill and Petit (*op. cit.*) .

In January 1965, during a surf clam cruise off Chincoteague Inlet, Virginia (Lat. N. 37°40′; Long. W. 75°15′) , two shells of adult *Cymatium poulsenii,* both measuring about 75 mm., were dredged up from 12 fathoms. The shells were inhabited by hermit crabs; although worn they still possess color and texture and do not appear to be fossils. If adult specimens are found alive at this latitude it will represent a significant advance northward from Cape Hatteras. — ARTHUR S. MERRILL, Bureau of Commercial Fisheries, Biological Laboratory, Oxford, Maryland and HUGH S. PORTER, Institute of Fishery Research, University of North Carolina, Morehead City.

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The Blue Whiting, *Micromesistius poutassou*, in the Western Atlantic, with Notes on Its Biology

David Miller

The blue whiting, *Micromesistius poutassou* (Risso), was first reported from the western North Atlantic in 1955. Since that time many more specimens have been taken over a steadily widening area. The most recent captures (1963) have provided sufficient material to make an initial assessment of its distribution and biology off the coast of eastern America. The blue whiting is now known from 570 miles of the Continental Slope from eastern Nova Scotia to southern New England over depths of from 100 to 275 fathoms. The number of specimens and the range over which they have been taken would seem to establish the species as a permanent resident of this area. Its apparent absence in the western Atlantic prior to the first report in 1955 may be explained by the fact that its normal geographic range barely overlaps the area regularly worked by the resident commercial fishing fleet.

THE blue whiting, *Micromesistius poutassou* (Risso), long known from the waters of the eastern Atlantic, was first recorded off New England waters by Bigelow and Schroeder (1955). Although only one other western Atlantic record (Scott, 1963) for this species has been published since that time, additional specimens have been taken. The recent catches (107 specimens, March–April 1963) warrant a summary of all known records and presentation of available information on the biology of this species in the western Atlantic.

Catches of blue whiting have been made on 10 different occasions since 1955, yielding a total of 119 specimens. In 1956, two specimens were taken from Georges Basin in the Gulf of Maine by commercial draggers out of Gloucester, Mass. The first was taken by the dragger "St. Anthony" at 41°57′ N, 68°08′ W, in 119 fms, 25 April and the second by the "Bonaventure" at 42°03′ N, 67° 50′ W, in 100 fms, 12 May. The Bureau of Commercial Fisheries R/V "Delaware" took one specimen on the Continental Slope south of Halifax, Nova Scotia on 1 October at 42°44′ N, 63°42′ W, trawling in 200 to 275 fms. Scott (1963) reported five specimens taken by R/V "A. T. Cameron" of the Fisheries Research Board of Canada at about 44° 00′ N and 59°00′ W in 1962. Between 15 March and 15 April 1963, Arthur Reis, captain of the dragger "Stephen R." out of Provincetown, Mass., landed 107 specimens. These fish were taken on five successive trips to an area 90 miles south of Martha's Vineyard (40°02′ N, 70°28′ W, 100 to 133 fms). Finally on 4 May 1964 the "Stephen R." took four specimens at 40°03′ N, 70°29′ W, in 110 to 135 fms. Captain Reis reported (pers. comm.) having taken about 100 blue whiting in the spring of 1963 and somewhat less than that the previous year while fishing the same area for silver hake, i.e., *Merluccius bilinearis* and *albidus.*

The catch localities for all known specimens of *M. poutassou* from the western Atlantic are given in Fig. 1. The distribution as defined by the records given here is interesting in that the majority of the speci-

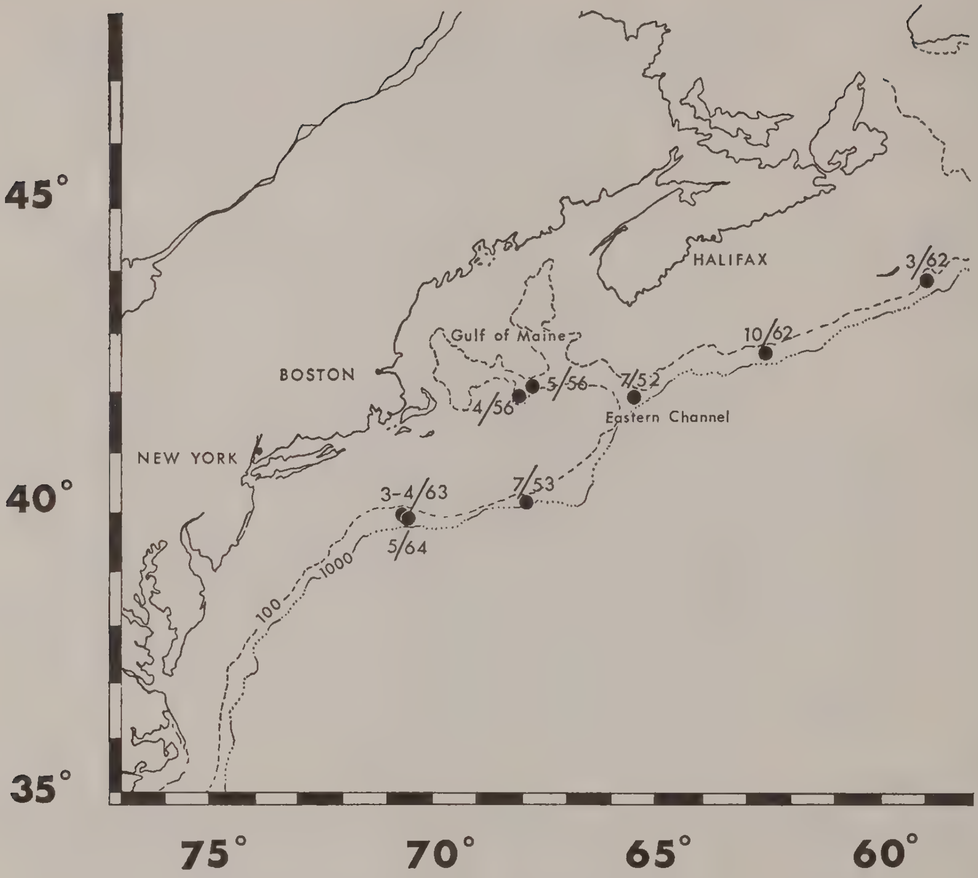

Fig. 1. *Micromesistius poutassou*, locality records from Western Atlantic (month(s) and year of capture noted).

mens are confined to a narrow band of water along the Continental Slope just outside of the 100-fm contour. It is not difficult to explain the presence of the two fishes taken in the Gulf of Maine. In terms of depth, the Eastern Channel provides access to the central Gulf from the Continental Slope. Further, the temperature and salinity regime at the bottom of the Gulf during the spring months (6° C and 34.5‰) closely approximates that of the adjacent slope water (6° C and 35.0‰). In fact, Bigelow (1928) pointed out that the deep water of the Central Gulf has its origin in the slope water, which enters by way of the Eastern Channel.

The number of catches since 1955 are now sufficiently large to confirm Bigelow and Schroeder's conviction that the blue whiting is a permanent resident of these shores. Also, the additional depth records strengthen their supposition that the inshore boundary of its regular range does indeed lie beyond the 100-fm isobath. These later catches extend the known geographic range some 310 nautical miles to the east and 120 to the west, so the *M. poutassou* has now been reported from 570 miles of the North American Continental Slope from the eastern tip of Sable Island Bank to just south of Woods Hole, Mass.

To determine whether the specimens taken by the "Stephen R." were in any way different from the four western Atlantic specimens described by Bigelow and Schroeder, measurements corresponding to theirs (*op. cit.*) were taken from 20 fish. A comparison of the two sets of measurements showed no significant differences, with one exception. In five of the 20 fish, the first pelvic ray was produced into a long filament increasing the

TABLE 1. AGE–LENGTH RELATIONSHIP, *Micromesistius poutassou.*
(Figures in parentheses from Saemundsson, 1929.)

Age-groups	I			II			III			IV			V			VI		
Sex	♂	?	♀	♂	?	♀	♂	?	♀	♂	?	♀	♂	?	♀	♂	?	♀
SL cm																		
36															1			
35															2			
34															1			
33												1	1		1			1
32												3			2			
31												7	1					
30										9	(1)	2						
29							1			7	(1)	5						
28							1		(2)	3		2						
27									(4)	2								
26							(4)1		(4)									
25							(3)		(4)									
24					(1)		(3)		(1)									
23							(1)											
22																		
21																		
20																		
19																		
18		(1)																

normal length 1.6 to 2.0 times. This filament has not previously been described, nor does it appear in illustrations of this species given by Bigelow and Schroeder (*op. cit.*), Poll (1947), d'Ancona (1931), Jenkins (1925), Schmidt (1906), Smitt (1892), Moreau (1881), or Couch (1869). It would appear that this pelvic filament is either easily broken off or a highly variable feature of the species.

Data on length, weight, age, sex, maturity, and stomach contents were taken from 56 fish caught by the "STEPHEN R." on a single trip (15–16 April 1963). Although the sample is too small to insure adequate representation of the western Atlantic populations, the following fragmentary biological information is included inasmuch as it represents the only available data from these waters. The length–weight relationship is given in Fig. 2. The range and mean standard length for the males were 23 to 30 cm and 26.2 cm, respectively, and for the females 25 to 32 cm and 27.9 cm.

An attempt was made to determine the age composition of the catch. Contrary to the conclusion of Saemundsson (1929), who found the otoliths preferable to the scales in determining the age of Icelandic specimens of *M. poutassou*, otoliths proved to be more difficult to interpret. Unfortunately, all but six fish were scaleless as a result of being chafed in the trawl net. A comparison of scale–otolith pairs from each of these six fish was made. Ages determined from the otoliths were one to three years higher than indicated by the scales. The tendency to overread the otoliths stemmed from difficulty in fixing the position of the outer margin of the first year's growth zone. In fact, the central area contained from one to as many as four opaque and hyaline areas. The first annulus on the scales, however, was quite distinct. Accordingly, the limits of the first annulus in the remaining otoliths was fixed with reference to the six scale–otolith comparisons. The majority of the fish thus aged were in the IV-year group. Table 1 combines Saemundsson's data on Icelandic fish with the present material, giving a rough idea of the age–length relationship for the species. If the age interpretation is correct, the females would appear to be slightly larger than the males at any given age.

Of the 56 specimens examined in detail, 28 were males and 28 females. Of the males, six had spawned, 21 were in spawning condition, and one was immature. Of the females, 16 had completed spawning and 12 were in

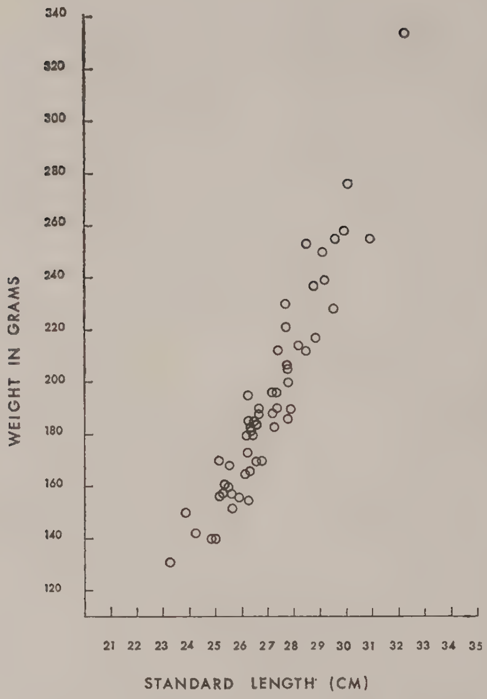

Fig. 2. *M. poutassou*, length–weight relationship.

spawning condition. Since just over 50% of the females examined had spawned by 15 April, a fair approximation of the spawning time in this latitude would seem to be 15 March to 15 May. This is in general agreement with Henderson (1957) and Schmidt (1909) who give March–May and late winter–early spring, respectively, for the spawning dates of the blue whiting in the eastern North Atlantic.

The fertilized eggs of this species have not yet been observed. However, Henderson (1957) described and figured a late stage egg which he reconstructed on the basis of measurements of prolarvae and a broken egg capsule. Ovulated eggs were found in the lumen of the ovary of one ripe female in the "Stephen R." collection. These eggs measured 1.0 to 1.1 mm in diameter and were without an oil globule. These observed diameters agree precisely with those proposed by Henderson.

Analysis of stomach contents indicated a highly specific, if monotonous, diet. All fish examined contained some food. Thirty-four contained a mixture of euphausiids (*Meganectiphanes norvegica*) and myctophids, 18 contained euphausiids only, and four, myctophids only. In one fish, containing euphausiids, a single hyperiid amphipod was found. Although fish in the stomach contents were in poor condition, one was identified as the myctophid *Hygophum hygomi*. Several less complete examples were identified on the generic level as *Hygophum*, while there was little doubt as to the familial affinities (Myctophidae) of the remaining. The stomach contents of the single blue whiting (416 mm SL), taken by the "Delaware," consisted of one rather well digested fish (195 mm SL) identified as *Paralepis* (most likely *coregonoides* or *atlantica*).

In characterizing the bathymetric distribution of the euphausiids, Calman (1909) stated that they were essentially pelagic animals. Fraser-Brunner (1949) similarly characterized the Myctophidae writing that their ecological relationships were in the upper layers of the ocean, or even at the surface. In referring to the depth range of the barricudinas, Rofen (1966) says that they occur from near the surface to middepths. Schmidt (1909) found that the stomach contents of *M. poutassou* in the eastern Atlantic always contained pelagic animals, mainly copepods and euphausiids. Thus, the bathymetric distribution of the food organisms found indicates a mesopelagic habit for this fish in its western as well as its eastern Atlantic range.

Captures by commercial fishing vessels have only been made during the spring or early summer from a narrow band of water just outside the 100-fm isobath (100 to 135 fms). The single specimen from 200 to 275 fms in October was taken by the R/V "Delaware." This suggests an inshore movement by the poutassou during the spring and a more offshore habitat during the remainder of the year. It also indicates a highly seasonal commercial availability. Since the New England commercial trawler fleet operates primarily within the 100-fm contour, its activities barely overlap the shoreward fringe of the blue whiting's range in the spring. During this time of the year the vessels tend to concentrate their activities toward the more shallow central parts of the fishing banks in their search for spawning concentrations of haddock. Thus, at the time blue whiting are available the vessels seem to be drawn away from the edge of the shelf toward shoaler water. Although Tåning (1958) suggested that the blue whiting was a relative newcomer to the western Atlantic, it seems more likely that its late appearance has been a function of the negligible fishing effort in its preferred habitat.

Assuming that the lower salinity preference of 35.25‰ given by Schmidt (1909) for this species holds equally well in the western Atlantic, the preferred locale of the blue whiting can be described as the middepths of waters bordering the Continental Slope from western Greenland southwestward to Cape Hatteras, North Carolina. Future exploratory fishing should reveal a relatively continuous distribution over this general area.

The author wishes to thank Captain Arthur Reis and the crew of the "STEPHEN R." for their continued interest and cooperation in bringing to port unusual specimens taken during their regular fishing operations. Sincere thanks are also due my former coworker, Robert R. Marak, for his analysis of the stomach contents, and to Richard Haedrich and Richard H. Backus of the Woods Hole Oceanographic Institution; the former for his identification of the Myctophidae and the latter for his kindness in reviewing the manuscript.

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A NEW LOCALITY RECORD FOR THE LANCELET, *BRANCHIOSTOMA CARIBAEUM* (SUNDEVALL), ON THE TEXAS COAST. A survey of the literature reveals that the lancelet, *Branchiostoma caribaeum* (Sundevall), ranges from Chesapeake Bay to the northern Gulf of Mexico from Florida westward to Aransas Pass, Texas. Distribution records for *B. caribaeum* along the Gulf coast are sporadic. Bigelow and Farfante (*In*: Fishes of the western north Atlantic. Pt. 1. *Sears Found. Mar. Res.*, 1–28, 1948) stated that this lancelet occurs occasionally in large numbers on the coast of western and northwest Florida (as far as Pensacola). These authors considered *B. floridae* (Hubbs, *Occ. Pap. Univ. Mich.*, 105: 1–16, 1922), to which specimens from this area were previously assigned, a synonym of *B. caribaeum* and listed the range as extending from Chesapeake Bay to the West Indies. A small collection of lancelets made by T. E. Pulley in Lydia Ann Channel in Aransas Bay, Texas, was identified as *B. caribaeum* by Gunter and Knapp (*Tex. J. Sci.*, 3(1): 134–138, 1951). They (*op. cit.*: 138) also reported a collection of four taken by Mr. Cleburne A. Shultz from near the pier at the Institute of Marine Science, University of Texas, at Aransas Pass, Texas, and presumed them to be *B. caribaeum* although positive identification was not made. Hefley and Shoemaker (*Science*, 115(2976): 48, 1952) reported additional lancelets from the Chandeleur Islands of Louisiana and the Mississippi coast. This species has not previously been reported, however, from Gulf coastal waters between Aransas Pass and the Chandeleur Islands.

On July 17, 1963, 12 lancelets were captured in an Ekman dredge at the junction of the Gulf Intracoastal Waterway and the Houston Ship Channel in Galveston Bay, Texas, at Latitude 29° 21.8′ N., Longitude 94° 47.8′ W. The average depth was 42 feet and the bottom sediment was sandy fragmented shell with small amounts of silt and clay.

In removal of the sample from the dredge, a number of lancelets were found protruding about ¼ inch above the surface of the sediment. These lancelets ranged from 40 to 44 mm. long and averaged 42 mm.; weight ranged from 0.15 to 0.20 gram and averaged 0.18 gram. The identification of these specimens. *Branchiostoma caribaeum* (Sundevall), was confirmed by Robert H. Kanazawa, Division of Fishes, Smithsonian Institution. *Cornelius R. Mock, Bureau of Commercial Fisheries, Galveston, Texas. Contribution No. 197, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas.*

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JAMES W. MOFFETT

The general biology of the cyclostomes with special reference to the lamprey

It is difficult to speak of cyclostomes, particularly lampreys, in a coldly objective, zoological sense. The sea lamprey became an object of our concern when it entered the Great Lakes above Niagara Falls via the Welland Canal about 1921 (11). It was then a scientific curiosity, although some ichthyologists (13) warned of its capability to destroy stocks of valuable fishes. The record of its devastations since that time is remarkable (2, 4). Gone from Lakes Huron, Michigan, and Superior are lake trout stocks that supported a commercial fishery which yielded an average annual production of 15.5 million pounds. Reduced to complete or relative insignificance are the fisheries for several species of whitefishes, for walleyes, and for burbot. Upset completely is the ecological balance among species that existed in these lakes (18, 22).

Our studies of this parasite and of its relatives have been directed toward the discovery of methods of control. Consequently, I have considered the lamprey a pest—a disease—comparable in its effects on fishes to any of several plagues that have brought and still bring misery, death, and destruction to man. Despite the emotional attitude and the overwhelming urgency to find the lamprey's weaknesses, it was necessary to study as many of its attributes as were amenable to inquiry before effective control could be devised. It is the purpose of this paper to review what we have learned about this animal and its relatives, and to reflect the great respect I have developed for its tenacity to life, its adaptability, and its genetic capacity to meet successfully the various problems it has encountered in persisting for millions of years.

Position of the Cyclostomes in the Animal Kingdom

Lampreys and hagfishes, the two remaining representatives of many extinct cyclostomes, are grouped together in most systems of classification developed for the vertebrates. These classification systems appear to be made for convenience and orderliness primarily and for expression of evolutionary development secondarily. Assignment of evolutionary relations to a position of secondary importance is most undesirable. Records of relationships and evolutionary history are, nevertheless, so fragmentary that precise conclusions are not attainable. New discoveries in the fossil and living records of forms, particularly fishes, are supporting changes in classification and evolutionary history almost as fast as new schemes are devised. Because of the nature of the fossil record, classification has been based on morphological (skeletal) similarities. Frequently, these similarities are demonstrated also in the embryology of living forms. Little has been done, however, in the very promising fields of physiological function and biochemistry, genetic evolution, basic relationships of protein structures, and endocrine functions. It is in these areas of interest that major contributions to our understanding of the real evolution of organ systems and of organisms will be made. The evolutionary relationships among vertebrate ancestors, now so poorly understood, may be clarified fully by studies in the fields just listed (5, 9, 15, 19).

For purposes of this exposition, I have chosen essentially the classification compiled by Bailey (3). He established the following arrangement:

Phylum Chordata
  Subphylum Hemichordata
  Subphylum Urochordata
  Subphylum Cephalochordata
  Subphylum Craniata
    Class Agnatha - Jawless fishes - Cyclostomes
      Subclass Cephalaspidomorphi
        Order Petromyzoniformes or Petromyzontia
          Family Petromyzonidae - Lampreys
            Subfamilies Petromyzoninae - N. Hemisphere
              Mordaciinae - S. Hemisphere
      Subclass Pteraspidomorphi
        Order Myxiniformes or Myxinoidea - Hagfish
    Class Chondrichthyes - Cartilaginous fishes
    Class Osteichthyes - Bony fishes

Information on the Agnatha dates back at least 450 million years to Ordovician times. Fossils of ostracoderms, primitive fresh-water chordates, are common in deposits of that age, found mainly in England and Scotland. These jawless forms reached a relatively high level of abundance and a diversified morphological development by the end of the next geological age (Silurian). The ostracoderms were covered more or less by bony external plates and some of them apparently were adapted to a relatively active life rather than to burrowing habits. They possessed the single nostril between their eyes and also the pineal or median eye characteristic of the lampreys and hagfish. Evidence exists that some ostracoderms had bony skeletons from which certain investigators concluded that the cartilagenous skeleton of modern cyclostomes is a degenerative feature. The ostracoderms apparently were filter feeders like the larvae of lampreys.

Some form resembling the ostracoderms was ancestral to the lampreys and hagfishes. However, their evolutionary lines may have been separate as far back as the Silurian. Lampreys are said to have evolved from a Cephalaspid-like type but the hagfishes are thought to have been derived from the pteraspids. Regardless of their derivation, they are the only remaining representatives of the ostracoderm ancestry. By the end of the Devonian age, ostracoderms were extinct—apparently unable to compete successfully with the then common, jawed vertebrates. Knowledge of the evolutionary history of the lampreys and hagfishes after the ostracoderms became extinct would be of great value. It is inconceivable that they persisted to the present without change. It may be that as the bony and cartilagenous fishes began to dominate the Devonian age, lampreys and hagfishes developed parasitic or scavenging habits. Speculation could lead to many other intriguing guesses about the evolutionary progression of modern cyclostomes, but there is little point in this scientific dreaming without basic evidence.

Differences Between Lampreys and Hagfishes

Hagfishes and lampreys are not closely similar. Table 1 points out differences that are important to our consideration of their biology. Practically all of the part of this comparison which deals with hagfishes is taken from the papers by Bigelow and Schroeder (7, 8).

Habits of Hagfishes

In their reproduction and to some extent in their habits, the hagfishes tend to resemble the sharks. They are apparently burrowers when at rest but otherwise are active scavengers, feeding upon dead or injured fishes. They are especially pestiferous to fishermen using bottom nets and long lines. Hagfishes bore into caught fishes and eat everything but skin and bones. They are frequently taken inside fully or partially eaten fishes and also in pots baited with meat or offal. Hagfishes are known to feed on haddock, hake, cod, ling, herring, mackerel, sturgeon, and even

TABLE 1.—DIFFERENCES BETWEEN HAGFISHES AND LAMPREYS

	Hagfishes	*Lampreys*
Gill pouches	6-15 paired openings each internally to pharynx and externally either separately or through a single aperture	7 pairs, opening separately to exterior but internally to a special tube separate from pharynx
Barbels	Present	None
Fins	Single, continuous around tail	Separate, supported by rays
Mouth	Not funnel-like, no accessory teeth	Funnel-like with numerous horny teeth
Nostril	At tip of snout opening to mouth—entrance of water of respiration	Blind sac on dorsal surface —not open to mouth
Tongue	Evertible with two rows of rasplike teeth	Evertible, with various tooth patterns—works with labial teeth
Mucus pores	Prominent, segmentally arranged along each side	Absent, at least not prominent or segmentally arranged
Position of anus	Near posterior end	Anterior to caudal fin
Eye	Without lens or iris, not visible externally, degenerate	Present, well developed in adult with iris and lens
Branchial basket	Vestigial	Present, surrounds gill pouches
Semicircular canals	One	Two
Pancreas	Well-developed	Scattered follicles
Neural arches	Absent	Present but rudimentary
Intestine	Internal longitudinal folds	Spiral valve or when as fold resembling valve
Sex organs	Structurally hermaphroditic not functionally so	In adult completely separate
Development	Direct—no larval stage	Larval stage, metamorphosis complete, secondary sex characteristics in mature adults
Eggs	Large, few (19-30), shell with hooks, anchored to bottom in clusters	Small, many (thousands), no shell, deposited in freshwater streams
Habitat	No anadromy, exclusively marine	Anadromous or in fresh water, few species marine as adults, none marine as larvae
Feeding	Scavenger	Parasitic or nonparasitic as adult—some adults do not feed
Spawning	Mostly year round	Seasonally (spring)

mackerel sharks. In Norwegian waters they also prey upon marine annelid worms.

LAMPREYS—THEIR USES AND DISTRIBUTION

In contrast to the hagfishes, lampreys have been and still are used as human food throughout that part of the world where they occur. Great numbers of lampreys are taken from the estuaries and streams of Europe, Asia, Australia, and New Zealand. They are considered as special delicacies in northern Europe and among the Maoris of Australia. We have heard the story that Henry I of England died of a surfeit of lampreys. There must be something to these tales because similar deaths have been reported among the Maori chiefs (26).

Lamprey fisheries of Europe, chiefly for the river lamprey, *Lampetra fluviatilis,* have declined in recent years, mainly because of dams, pollution, and overfishing (23).

Early settlers in the United States caught lampreys for food as they migrated into New England streams from the ocean to spawn. Lamprey runs into New England streams now have disappeared or are very small. Construction of dams and diversion works has exterminated many populations that parasitized the fishes of the northwest Atlantic. Use of lampreys for food in the Soviet Union still supports larger fisheries in the rivers of the Baltic and Caspian seas. In the lower reaches of the Volga River, lampreys are caught in great numbers (6). The catches for 1910 were 16,900,000 specimens; for 1911, 23,700,000; for 1912, 24,500,000; and for 1913, 33,400,000.

American Indians on the Pacific Coast traditionally operated traps in coastal rivers to capture lampreys for food. Some traps in northern California streams still may be used. Large runs of lampreys pass up the fish ladders on Bonneville Dam across the Columbia River. In 1961, more lampreys were counted over the dam (364,805) than ever before. The lamprey was the commonest migrant, even outdoing the salmon.

Not all lampreys are parasitic or large enough to be used for food. Most species are small creek dwellers not more than eight inches long. When they reach adulthood through metamorphosis they do not feed. They persist long enough to spawn and then like all their kind they die. Lamprey larvae are good bait and can be dug from the soft muds of most streams. States usually prohibit such use to stop the spread of parasitic forms by fishermen.

Seven genera and about 30 species of lampreys are recorded from the temperate zones of the Northern and Southern Hemisphere. Two genera, *Geotria* and *Mordacia,* are found in Australia, New Zealand, Tasmania, and Chile (6, 26). *Petromyzon, Lampetra, Caspiomyzon, Ichthyomyzon,* and *Eudontomyzon* occur in the Northern Hemisphere (6). There are no records of lampreys from southern Africa; otherwise, taking one species or another, their distribution is circumpolar.

The genera *Petromyzon, Ichthyomyzon,* and *Lampetra* are in North America. Each genus has at least one parasitic species but only two genera, *Petromyzon* and *Lampetra,* have species that migrate to the sea. In North America, *P. marinus,* the sea lamprey, is found on the Atlantic Coast from the Maritime Provinces of Canada to Florida and is landlocked in the Great Lakes and Finger Lakes of New York. *L. japonica,* the Pacific lamprey, occurs in Alaska and down the Pacific Coast to Mexico.

Our interests center upon those lampreys that occur in the Great Lakes drainage. They are discussed by Hubbs and Lagler (12), Trautman (24), Vladykov (25), Hubbs and Trautman (14), and other authors. Five species are recorded from the Great Lakes area.

- *I. unicuspis* Hubbs and Trautman. The silvery lamprey (parasitic, limited migration).
- *I. fossor* Reighard and Cummins. The northern brook lamprey (nonparasitic, very little or no migration).
- *I. castaneus* Girard. The chestnut lamprey (parasitic, slightly migratory).
- *P. marinus* L. The sea lamprey (parasitic, migrates extensively, moves to the sea when not landlocked).
- *L. lamottei* (Lesueur). The American brook lamprey (nonparasitic, nonmigratory).

NATURAL HISTORY OF LAMPREYS

All the lampreys in the Great Lakes basin and, for that matter, lampreys of the world have a broadly similar life history, made up of three rather distinct phases—egg, larval, and "adult" stages.

Eggs are spawned in nests which, generally described, are depressions in sand or gravel built by adult lampreys in relation to the hydrodynamics of the site selected. The type of material in which lampreys build nests depends to a great extent on the size of the adults. Smaller lampreys use sand and smaller gravel; larger lampreys usually prefer larger gravel mixed with sand. Spawning is in late spring and early summer. Some spawning may occur in midsummer but it is usually inefficient because of high water temperatures. The river lamprey of Europe spawns in the spring but migrates to the spawning grounds in late fall and early winter (6). Zanandrea (28) reported that spawning for certain nonmigratory species in Italy may begin in February. No domestic forms migrate into streams much in advance of spawning time. Nonmigratory, nonfeeding species, however, metamorphose from the larval stage and appear to be sexually mature by midwinter.

The larval stage of all the species is closely similar. Following the incubation of the eggs and early development of the larvae, which varies in duration in relation to water temperature, the small ammocetes emerge from the nest, drift downstream, and establish themselves in silty or sandy bottom. Generally speaking, the type of bottom selected is more silty when the lampreys are small and sandier as the lampreys become larger. Some of our studies indicate that larvae move about over the stream bottom at night. Marked individuals have been taken as far away from the site of marking as one mile; some have been taken upstream from the marking site as much as half a mile. Downstream drift resulting from floods, freshets, and from willful change of habitat is common. Larvae move from stream mouths onto stream deltas in the Great Lakes and are distributed along some lake shores adjacent to stream mouths. Whether they are able to complete their life history there is unknown. Larval life of species in the Great Lakes basin lasts at least four years. The actual duration of larval life for any of the species has not been established. Applegate (1), Wigley (27), and others have attempted to identify age groups of sea lamprey larvae from length-frequency distributions but results are not very conclusive. It appears that the length of larval life is not constant. States of nutrition and climate undoubtedly influence growth rate of larvae and hence the time of onset of metamorphosis.

Larvae of those species which do not feed as adults usually grow larger than those that ultimately become parasitic. In all species, larvae lose some length during metamorphosis. None of them feed during this period. Food of the larvae is rather uniform regardless of species. Creaser and Hann (10) described the food of larvae taken in midsummer as predominantly diatoms and desmids with admixtures of Protozoa, filamentous green algae, detritus, and pollen. Schroll (20) indicated in a rather extensive work on Australian lampreys that the larvae of the two species studied confined their diet to diatoms in spring, summer, and fall and included some detritus in the winter food. He attempted to demonstrate that larvae were very selective in their feeding; they were actually killed by ingestion of *Paramoecium*, artificial fish food, chopped nematodes, and Tubificidae. Experiences of others, such as Sterba (23), do not confirm the degree of selectivity in feeding described by Schroll but all studies show a predominance of diatoms and detritus in the larval diet.

Larvae are capable of surviving extreme periods of starvation or of inadequate feeding. Experiments in our laboratory have demonstrated that sea lamprey larvae 105 mm long can persist for at least one year with only such food as is available in unfiltered Lake Huron water. A group of 50 larvae lost an average of 9.6 mm in length and suffered a mortality of 8% in 48 weeks. A similar group fed yeast twice weekly gained 15.5 mm and suffered the same mortality. Larvae of the fed group began to metamorphose between the 48th and 60th week of the experiment. None of the unfed larvae showed signs of metamorphosis. They began to die in significant numbers between the

50th and 78th weeks. Finally, after the 78th week the single larva left in the unfed group began to grow. Such tolerances among larvae would lead one to conclude that the duration of larval life is extremely flexible. We are fairly confident that the onset of metamorphosis of larvae is not entirely a function of time and that as a year class of larvae develops to metamorphosis, only a portion of this year class transforms in the first year, another portion in the second.

In a sense lampreys have two life histories, one as sedentary filter feeders (larvae) restricted to the bottom of streams and another as active adults in which parasitism may or may not occur but during which reproduction is accomplished. Zanandrea (28) has observed neoteny (sexual development in the larvae) in samples of ammocetes taken from Fibbio Brook, near Verona, Italy. The neotenic specimens, all females, were collected during the spawning season. In some collections 20% of the female ammocetes gave certain evidences of neoteny. Some larvae showed well-developed principal secondary sexual characters, namely, enlargement of the two dorsal fins, development of the anal pseudofin, and transparent appearance of the body wall through which ovaries and eggs in advanced development could be seen. He has never found this phenomenon in other streams sampled in Europe nor did he mention that such maturity ever occurred in males. An extensive review of the literature on lamprey life history has disclosed no other examples of neoteny. I have checked our records of thousands of ammocetes from many areas around the Great Lakes and find no evidence of neoteny. It may be, however, that these tendencies have escaped our notice. From the occurrence of neoteny, one is tempted to speculate that perhaps at one stage in the evolution of lampreys their life history was completed in the larval stage. Perhaps metamorphosis is a more recent development initiated by acquisition through evolution of a more sophisticated endocrine system (15, 23). Various authorities believe that metamorphosis is stimulated by pituitary-like hypophyseal secretions. Leach (15) believed that amphioxus, a marine species, used widely as a type of primitive vertebrate, has remained essentially larval-like because of the degeneration of its nervous system. The forebrain, the midbrain, and hypophysis have been lost. With the loss of the latter, the capacity to metamorphose, if it were ever a characteristic of amphioxus, was also lost.

Of the five species of lampreys in the Great Lakes basin, two, the northern brook lamprey (*I. fossor*) and the American brook lamprey (*L. lamottei*), have relatively short life after metamorphosis. Members of these species metamorphose to adults which look, superficially at least, like the adults of any other species at this stage except that they are somewhat larger. They do not feed, however, but remain relatively sedentary in the streams as long as five months and become sexually mature without increasing in size. All of them spawn in the spring and die shortly thereafter. Those species which are parasitic vary in migratory habits after transformation. The sea lamprey undertakes the greatest migration. The silver lamprey, *I. unicuspis,* also migrates to the large lakes. All of the juvenile parasites drift downstream through late fall, winter, and early spring. Heaviest migration is usually in two periods, one in the fall and another in early spring. The number of migrants in each period seems to depend somewhat on the stream discharge. Usually, the downstream movement in the fall is the dominant one in streams tributary to Lake Superior.

Once the sea lamprey reaches the Great Lakes it spends 12-20 months feeding on fishes before it returns in early spring to the streams to spawn. We have not been able to demonstrate the development of any homing instinct among the sea lampreys in the Great Lakes. It is clear that during their establishment and expansion there could have been little homing. Had there been, the rapid and spectacular spread of this species to all of the lakes (a period of 25 years) and to practically all of the streams usable for spawning in each lake would not have taken place.

Our opportunity to study the adult life of the sea lamprey in the Great Lakes has been limited because of their relatively wide dispersal. Sea lampreys marked at given localities in the Great Lakes have been recovered at widely separated points. We suspect that part of this dispersal occurs when lampreys attach to prey fishes and to ship hulls and remain there as they move about the lakes. Dispersal is so rapid and has so little pattern that other conclusions are unattractive (21).

Two generations of metamorphosed sea lampreys were reared to maturity in our laboratory. One of the most significant results from this undertaking was the rather drastic effects of lamprey feeding on the blood composition of the host fishes (16). To generalize, blood of the host fishes under normal conditions contained 1 to 1¼ million red cells per milliliter. After sea lampreys had fed on these fishes to the point where death was imminent, the red cell counts were frequently below 300,000 per milliliter. Also, the clotting time of the blood was very short.

The cytolytic action of lamprey saliva makes possible the utilization of some fish tissue other than blood and body juices (16). The mere injection of lamprey saliva under the skin of a sound fish produces a pit which resembles a lamprey wound once the skin over it is removed and the liquified tissue is drained off. The base below such a wound appears to consist of relatively sound flesh.

It has been said frequently that the food of adult lampreys consists of things other than blood and body tissues. Bases for these statements refer to findings in lamprey guts of fish eggs, invertebrates, and algae. We have observed repeatedly that lampreys, attached to that portion of a fish adjacent to the coelom, do penetrate into the body cavity and ingest eggs from ovaries, even stomach and intestinal contents when the digestive tract is perforated. Various acanthocephalid worms in the intestines of adult sea lampreys may indicate that contents of the host's digestive tract are often ingested by the lamprey when deep penetration into the coelom occurs (17).

When lampreys become sexually mature they undergo what might be called a second and to some degree degenerative metamorphosis. The digestive system becomes nonfunctional and, with the exception of the liver, literally shrinks to a vestige. Color patterns change and many lampreys become blind. The tendency to be negatively phototrophic so characteristic of immature and migrating lampreys disappears upon full maturity. Male lampreys develop ridges down the midportion of their backs and females develop certain nodes that are said to assist in the reproductive act.

It was hoped that sea lampreys landlocked in fresh water might ultimately degenerate to the point where they would become relatively harmless. Adults of landlocked sea lampreys are much smaller at maturity than their counterparts in the ocean. The dwarf races of the sea lamprey in the Finger Lakes of New York are smaller on the average than the landlocked stocks in the Great Lakes. This difference may not persist since the sea lampreys in the Great Lakes have not had everything working in their favor. During the initial growth of its populations in each of the Great Lakes, numbers of sea lampreys increased almost geometrically until a peak was reached. After the peak was attained, characteristic depression below the peak ensued and then a general leveling off in numbers followed. Following the initial buildup of the sea lamprey, length and weight of mature individuals diminished. This reduction has amounted to as much as 3 inches in length (from 19 to 16 inches) and several ounces in weight in lampreys from Lakes Michigan and Huron over the last 15 years. Despite this tendency toward smaller size, these lampreys are fully mature and reproduce successfully. Larger sea lampreys produce more eggs than smaller ones and the reduction in egg volume over the whole population has been rather large as the adults have become smaller. The possible yield of eggs in some stocks has dropped at least ⅓ but this change does not seem to have affected the ultimate production of ammocetes.

Hope is scant that the handicaps of life in fresh water will be sufficient to reduce to insignificance the effects of the sea lamprey as a parasite on the fishes we want for ourselves. If no control were placed on the lamprey's numbers, no economic fishery could be founded on the fishery resources the lamprey might spare. The sea lamprey's appetite is too large and its adaptability too great for us to consider its effect a temporary incident in the history of fishing on the Great Lakes.

PART V — GENERAL BIOLOGY OF THE LAMPREY

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Records for Parabornia squillina. — Moore (1961. Gulf Research Reports, *1*(1), 58 pp.) noted a small bivalve which was tentatively referred to the genus "Lepton" on the stomatopod crustacean, *Lysiosquilla scabricauda* (Lamarck), in Mississippi. Boss (1965. Amer. Mus. Novitates, no. 2215, 11 pp., 3 figs.) described *Parabornia squillina* as a commensal erycinid attached to the ventral surface of the abdomen and thorax of *L. scabricauda* from the Caribbean coast of Panama. Boss ([*in press*]. Malacologia. Symbiotic Erycinacean Bivalves) indicated that Moore's "Lepton" is *P. squillina.* The present note is to record additional specimens and measurements of *P. squillina* and to document its range. Four specimens of this bivalve were taken by W. Demoran from *L. scabricauda* collected at Horn Island, Mississippi, and another six individuals were recovered in the same area from *L. scabricauda* collected at Dog Keys Pass, Mississippi. Two of the specimens are larger than any in the type series and are 7.48 mm. × 4.90 mm. × 2.28 mm. and 7.32 mm. × 4.88 mm. × 2.28 mm. respectively. — D. R. MOORE, Institute of Marine Science, University of Miami, Miami, Florida, and K. J. BOSS, Ichthyological Laboratory, Bureau of Commercial Fisheries, Washington, D. C. Contribution No. 673 from the Marine Laboratory, Institute of Marine Science, University of Miami.

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Notes on the Coloration and Behavior of the Common Dolphin, *Coryphaena hippurus*

A. Earl Murchison and John J. Magnuson[1]

While studying scombrid fishes at the Kewalo Basin tank facility of the U. S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii, we noted similarities between the behavior of the common dolphin, *Coryphaena hippurus* Linnaeus, and that of the scombrids. These similarities led us to observe the coloration, swimming speed, and behavior of *C. hippurus* incidentally to the studies on scombrids.

Most observations were made on five captive specimens in shoreside tanks during July–September 1962. Additional observations were made at sea through underwater viewing ports from a raft.

The *C. hippurus* specimens had been caught by trolling with barbless hooks, transported in a baitwell of a commercial fishing boat, and transferred at shore by dip net to a portable 2300-l tank from which they were allowed to swim directly into the shoreside tank in the manner described by Nakamura (1962, Copeia 1962 (3):449–505). The outdoor tank was circular, 24 ft in diameter, and 3½ ft deep, and had an observation window in its wall. Water temperature in the tank was about 24° C during the day and 22° C at night. Salinity was 33‰.

All five fish eventually jumped out of the tank and died, the last after 45 days in captivity.

The *C. hippurus* averaged 76 cm in fork length and 3.7 kg in weight. They were fed 5–7-gm pieces of beef liver and whole thawed night smelt, *Spirinchus starksi* (Fisk), which weighed approximately 12 gm. When fed at 24-hr intervals, the fish ate 334 gm per feeding, approximately 9% of the body weight.

Although *C. hippurus* have been reported by many authors to exhibit a changing array of many brilliant colors, their basic coloration in the tanks and at sea varied between two extremes. One was a silver-blue phase similar to that illustrated by the Fisheries Society of Japan (1931, Illustrations of Japanese Aquatic Plants and Animals, I, Pl. XXX). The other extreme was a yellowish phase similar to that illustrated by Walford (1937, Marine Game Fishes of the Pacific Coast, Alaska to the Equator, Univ. Calif. Press, Berkeley, Pl. 43) and noted by Gibbs and Collette (1959, Bull. Mar. Sci. Gulf Carib. 9(2):122) and Rothschild (1964, Copeia 1964 (2):445–447). Intermediate shades between these two extremes occurred. The intermediates were various hues of greenish-blue or greenish-yellow and apparently resulted from the combined effects of the blue and the yellow coloration.

In the extreme silver-blue phase the body and caudal fin were silver-blue. The extreme ventral body surface was silver-white. The dorsal fin, the dorsal surface of the pectoral fins, and the lateral surfaces of the pelvic fins were blue. Dark blue spots 3–5 mm in diameter were scattered over the body.

In the extreme yellow coloration, more evident at sea than in tanks, the caudal fin, the anal fin, the outer surface of the pelvic fins and the dorsal surface of the pectoral fins turned bright yellow while the head and body turned greenish-yellow. The same dark-blue spots were present.

C. hippurus observed through underwater viewing ports from a raft, *Nenue,* described by Gooding[2] tended to take on the yellow coloration just after reacting to food or just after a transient barred coloration described below faded. The yellow coloration also occurred while *C. hippurus* were struggling on a hook and line or lying on the deck just after capture.

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[1] U. S. Fish and Wildlife Service, Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii 96822. Manuscript received May 18, 1965.

[2] Gooding, Reginald M. 1965. A raft for direct subsurface observations at sea. U. S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 517. 5 p.

The broad dark vertical bars described by Strasburg and Marr (1961, Copeia 1961 (2): 226–228) were observed in the tank only once and then they were faint. These alternate dark and light vertical bars about 5 cm wide formed on the lateral surfaces of the *C. hippurus* when a live 25-cm *Tilapia mossambica* was tossed into the tank after the *hippurus* had not been fed for 10 days. The bars were displayed during an attack by the *hippurus* which ended with the consumption of the *T. mossambica.* A more prominent barred coloration was observed at sea after chopped meat was tossed in front of two *hippurus* swimming around the observation raft, and while the *hippurus* were attacking species of smaller fishes congregated at the raft.

The *hippurus* in the tanks swam continuously day and night with an undulating body movement, mouth agape and pectoral fins extended. During turns of 90° or sharper, the dorsal fin was raised slightly. The left pelvic fin was extended during gradual left turns; the right during gradual right turns. The typical swimming speed of a 71.1-cm *hippurus,* measured on three different days over a one-week period, was 56.3 cm/sec (0.79 body length/sec) (95% confidence interval:54.8–57.8 cm/sec; $n = 31$ 30-sec observations, $s^2 = 19.32$). At this speed approximately 50 km would be traversed in a 24-hr period. The typical tail-beat frequency was 1.21 beats/sec (95% confidence interval:1.10–1.32 beats/sec; $n = 31$, $s^2 = 0.09256$). A tail beat is defined as a complete cycle back and forth. At the typical speeds the fish was moving 46.5 cm/tail beat or 0.654 body length/tail beat. Motion pictures taken from the raft showed the average tail-beat frequency of *C. hippurus* about 100 cm in fork length swimming near the raft to be 1.20 beats/sec (95% confidence interval:1.14–1.27 beats/sec; $n = 8$, $s^2 = 0.009143$), essentially the same as in the tank. The surface temperature was 27° C, only 3° C higher than the daytime tank temperatures.

These slow rates of swimming are those most commonly observed for *C. hippurus* both in tanks and at sea. Since they never stop swimming, these are as close to resting speeds as the animal attains. These dolphins apparently irrigate their gills by forward progression through the water and maintain swimming depth by the hydrodynamic lift exerted against the pectoral fins. They do not have a gas bladder. These same functional components (respiration and hydrostatic equilibrium) of locomotion in pelagic fishes have been noted previously for scombrids (Breder, 1926, Zoologica 4(5):159–297; Hall, 1930, Am. J. Physiol. 93(2):417–421; Magnuson and Prescott[3], Nakamura, op. cit.) and are probably a very common adaptation of locomotion in pelagic fishes.

Several characteristic behavior patterns were observed among the *C. hippurus* in captivity. These were named mouth closure, oral valve closure, yawn, lean, chafe, jerk, and defecation. All of these, plus surfing, also were observed at sea. Their occurrence both in captivity and at sea suggests that they are naturally occurring behavior patterns in the repertoire of *C. hippurus.* A brief description of each, based primarily on the tank observations, is presented here.

Mouth closure. The mouth is closed completely for 1–5 sec and then reopened to the typical 2- to 5-cm gape.

Oral valve closure. For periods of less than 1 sec, the mouth is closed partially from the typical gape in such a way that the oral valve appears to close completely. The mouth then is reopened to the typical gape.

Yawn. The mouth is opened maximally, the gular region is depressed, the opercles are flared, all fins are extended, and all caudal motion is stopped. Typical posture and locomotion are disrupted for 3–4 sec.

Lean. The body is tipped to the side at angles of 45–90°. Sometimes this results during a turn as a continuation of a banking posture, but occasionally it results from a quick tipping movement while following a straight course. Then the dorsal fin is extended, as are the pectoral and pelvic fins on the side toward the surface.

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[3] Magnuson, John J., and John. H. Prescott. 1966. Courtship, locomotion, feeding and miscellaneous behaviour of Pacific bonito (*Sarda chiliensis*). Anim. Behav. 14(1):54-67.

This swimming posture is maintained for 3–10 sec and ends with a sudden return to the upright swimming posture.

Chafe. While swimming past an object, the fish brushes or rubs the lateral body surface against the object. If the chafe is directed against the tank's standpipe or sides, the normal upright swimming posture is maintained, but if the object chafed against is above the dolphin, the chafe occurs in conjunction with a lean.

Jerk. A single shudder or quiver passes over the body without visibly affecting locomotion.

Defecation. A brownish-green cloud of fine material was ejected for a 1–3 sec period during typical swimming behavior.

Surfing. The fish swims downwind just beneath the surface, positioning itself in front of a wave crest. The anterior-posterior axis of the body is inclined from the horizontal at approximately the same angle as the lead surface of the wave. With little or no caudal movement the fish travels rapidly forward in a horizontal plane at the same speed as the wave crest.

The mouth closure, yawn, lean, and jerk of *C. hippurus* appear very similar to patterns observed in another pelagic fish, the Pacific bonito *Sarda chiliensis* (Cuvier) (Magnuson and Prescott, op. cit.). Other similarities are the transient vertically barred coloration, shared also with the skipjack tuna, *Katsuwonus pelamis* (Linnaeus) (Nakamura, op. cit.), and continuous swimming. These similarities in behavior between a coryphaenid and a scombrid suggest that the functions may also be the same and are perhaps common to many pelagic predaceous fishes.

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LENGTH-WEIGHT RELATIONS OF PACIFIC TUNAS

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ABSTRACT

Graphs of the length-weight relations of skipjack tuna (Katsuwonus pelamis), yellowfin tuna (Thunnus albacares), bigeye tuna (T. obesus), and albacore (T. alalunga) are based on unpublished data of the U.S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu. Published and unpublished data on the length and weight of Pacific tunas are summarized in tables.

Data on length-weight relations of four species of Pacific tunas have been gathered from published papers and from the files of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu. They are presented in the following tables and figures:

Species	Table	Figure
Skipjack tuna (Katsuwonus pelamis)	1	1
Yellowfin tuna (Thunnus albacares)	2	2
Bigeye tuna (Thunnus obesus)	3	3
Albacore (Thunnus alalunga)	4	4

The figures are based on previously unpublished data collected from tunas in the central Pacific by the staff of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu.

With one exception, the original calculations were based on the usual formula:

$$W = aL^b$$

or

$$\log W = \log a + b \log L,$$

where W is weight, L is fork length (except for Schaefer's formula for yellowfin tuna, where it denotes total length), and a and b are constants. For the data on yellowfin tuna, Hiratsuka and Morita (1935) reverse the relation:

$$L = aW^b$$

or

$$\log L = \log a + b \log W.$$

Conversion factors that may be useful are:

1 lb. = 0.4536 kg.
1 kg. = 2.2046 lb.

ACKNOWLEDGMENTS

We thank Harold B. Clemens and William H. Baycliff for their careful reviews of the tables.

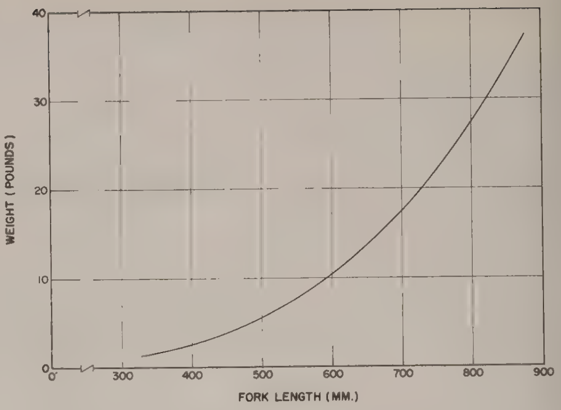

Figure 1.--Length-weight relation of skipjack tuna: Log Weight = -8.34241 + 3.36836 Log Length; number, 1,298; range, 327-877 mm.; collection period February 1948-December 1960; from files of the BCF Biological Laboratory, Honolulu.

Table 1.--Summary of data on length-weight relation of skipjack tuna

Locality	No. of fish	Size range of fish		log a	a	b	Weight unit	Length unit	Source	Comments
		Weight	Length							
Bonin Islands (Ogasawara)	268	--	--	-0.68825	0.205	3.67	gm.	cm.	Uda (1941)	--
Northeast coast of Japan	20	--	30-60 cm.	-1.94693	0.0113	3.16	gm.	cm.	Kawasaki (1952)	--
Hawaii	268	2-1/2-12-1/2 lbs.	--	-4.7262	1.878×10^{-5}	3.2164	lb.	cm.	Tester and Nakamura (1957)	--
Eastern tropical Pacific	924	2.56-19.25 lbs.	393-714 mm.	-8.437	3.652×10^{-9}	3.403	lb.	mm.	Chatwin (1959)	--
Eastern tropical Pacific	1,280	2.56-19.25 lbs.	393-714 mm.	-8.424	3.763×10^{-9}	3.265	lb.	mm.	Hennemuth (1959)	Includes data of Chatwin (1959).
Philippines	189	--	345-655 mm.	-4.48585	3.267×10^{-5}	3.09569	lb.	mm.	Ronquillo (1963)	Males only. Data from Ronquillo's fig. 26 not from table XI or from fig. 25.
Philippines	151	--	340-627 mm.	-4.70421	1.976×10^{-5}	2.96482	lb.	mm.	Ronquillo (1963)	Females only. Data from Ronquillo's fig. 27 not from table XI or from fig. 25.
Central Pacific	1,298	--	327-877 mm.	-8.34241	4.546×10^{-9}	3.36836	lb.	mm.	BCF Honolulu	--

Table 2.--Summary of data on length-weight relation of yellowfin tuna

Locality	No. of fish	Size range of fish		log a	a	b	Weight unit	Length unit	Source	Comments
		Weight	Length							
?	44	5-60 kg.	--	1.60325	40.12	.33	kg.	cm.	Hiratsuka and Morita (1935)	Formula: $L=aW^b$
Pacific coast of Costa Rica	93	--	542-1,571 mm.	-7.56225	2.74×10^{-8}	2.940	kg.	mm.	Schaefer (1948)	Total length used instead of fork length
Eastern tropical Pacific	541	4.75-72.00 lbs.	476-1,149 mm.	-7.40961	3.894×10^{-8}	3.020	lb.	mm.	Chatwin (1959)	--
Hawaii	59	1-17-3/4 lbs.	--	-4.2015	6.288×10^{-5}	2.9045	lb.	cm.	Tester and Nakamura (1957)	--
Japan	about 10,000	--	--	-2.17884	6.640×10^{-3}	3.1878	gm.	cm.	Kamimura and Honma (1959)	Dressed weights used
Philippines	99	--	827-1,840 mm.	-4.62856	2.352×10^{-5}	2.84682	kg.	mm.	Ronquillo (1963)	Males only. Data from Ronquillo's text not from table XI or from figs. 11 and 12
Philippines	43	--	1,096-1,530 mm.	-4.36432	4.322×10^{-5}	2.87651	kg.	mm.	Ronquillo (1963)	Females only. Data from Ronquillo's text not from table XI or from figs. 11 and 12
Philippines	106	--	320-828 mm.	-3.09437	8.047×10^{-4}	2.73643	lb.	mm.	Ronquillo (1963)	Males only. Data from Ronquillo's fig. 32 not from table XI or fig. 31
Philippines	78	--	472-805 mm.	-4.98801	1.028×10^{-5}	2.78797	lb.	mm.	Ronquillo (1963)	Females only. Data from Ronquillo's fig. 33 not from table XI or fig. 31
Central Pacific	4,822	--	70-180 cm.	-4.48732	3.256×10^{-5}	3.05834	lb.	cm.	BCF Honolulu	--

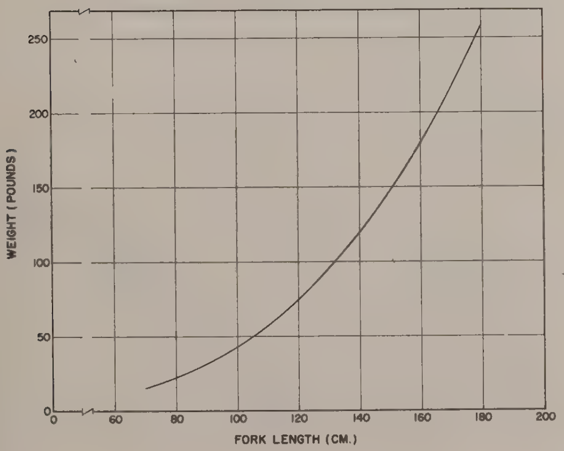

Figure 2.--Length-weight relation of yellowfin tuna: Log Weight = -4.48732 + 3.05834 Log Length; number, 4,822; range, 70-180 cm.; from files of the BCF Biological Laboratory, Honolulu.

Table 3.--Summary of data on length-weight relation of bigeye tuna

Locality	No. of fish	Size range of fish		log a	a	b	Weight unit	Length unit	Source	Comments
		Weight	Length							
Philippines	27	--	1,120-1,859 mm.	-4.32003	4.786×10^{-5}	2.94430	kg.	mm.	Ronquillo (1963)	Males only. Data from Ronquillo's fig. 14 not from table XI or from fig. 13.
Philippines	28	--	1,050-1,704 mm.	-4.76422	1.721×10^{-5}	2.74669	kg.	mm.	Ronquillo (1963)	Females only. Data from Ronquillo's fig. 14 not from table XI or from fig. 13
Central Pacific	9,144	--	80-190 cm.	-4.09305	8.071×10^{-5}	2.90182	lb.	cm.	BCF Honolulu	--

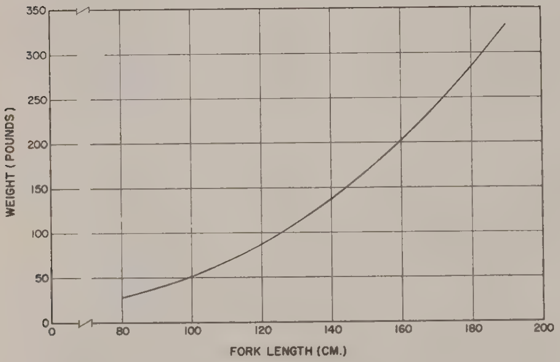

Figure 3.--Length-weight relation of bigeye tuna: Log Weight = -4.09305 + 2.90182 Log Length; number, 9,144; range, 80-190 cm.; from files of the BCF Biological Laboratory, Honolulu.

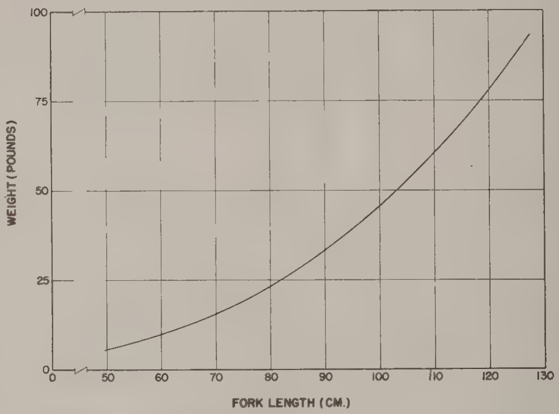

Figure 4.--Length weight relation of albacore: Log Weight = -4.24241 + 2.94950 Log Length; number, 200; range, 49.6-127.6 cm.; from files of the BCF Biological Laboratory, Honolulu.

Table 4.--Summary of data on length-weight relation of albacore

Locality	No. of fish	Size range of fish		log a	a	b	Weight unit	Length unit	Source	Comments
		Weight	Length							
Eastern Pacific	29,474	--	50-85 cm.	-4.912	1.225×10^{-5}	3.13	kg.	cm.	Partlo (1955)	--
Eastern Pacific	1,073	--	38-100 cm.	-7.30662	4.936×10^{-8}	2.99	lb.	cm.	Clemens (1961)	--
Hawaii and northern Pacific	200	--	49.6-127.6 cm.	-4.24241	5.722×10^{-5}	2.94950	lb.	cm.	BCF Honolulu	--
Samoa-landed	887	--	78-108 cm.	-3.7101	1.949×10^{-4}	2.6822	lb.	cm.	BCF Honolulu	--

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AMERICAN SHAD...A SPRINGTIME DELICACY

Shad, like salmon, migrate thousands of miles in the ocean and return to their natal stream to spawn, but how and by what mechanism they are guided remains a mystery.

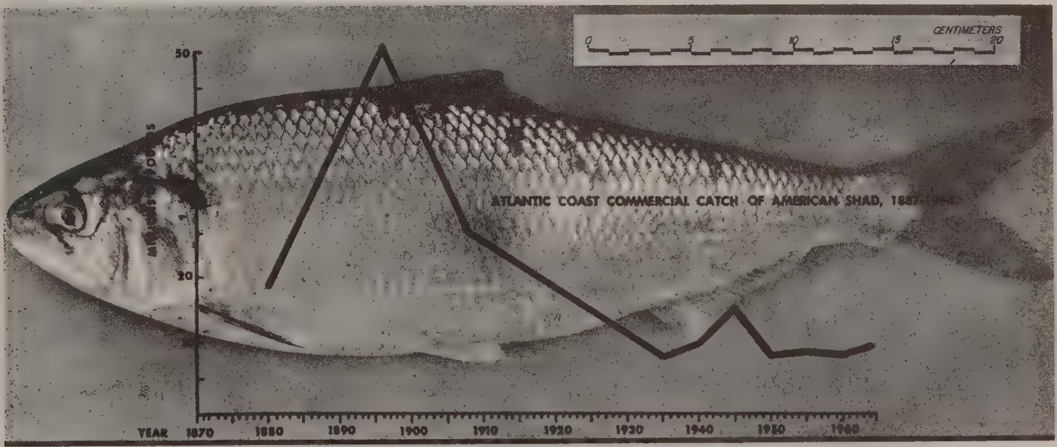
This fish, of the herring family Clupeidae, with the scientific name *Alosa sapidissima* (Wilson) and common names "White Shad," "Poplarback Shad," and just plain "Shad," is found throughout its range in sufficient quantities to give rise to fisheries of great economical and recreational values. The appearance of this fish in the fresh fish markets is a sure sign of spring. On the Atlantic Coast, it is distributed from the Gulf of St. Lawrence, Canada, to St. Johns River, Fla., and is most abundant from North Carolina to Connecticut. Many attempts to introduce the species in waters where it is not native, such as the Mississippi drainage and tributaries to the Great Lakes and Great Salt Lake, have failed. It was successfully introduced in the Sacramento and Columbia Rivers on the Pacific Coast in the 1870's and now occurs from the Mexican border to Cook Inlet, Alaska. Because little information is available on the Pacific Coast stocks, this report is primarily about the species on the Atlantic Coast.

Largest of the Clupeids

The species is the largest and best known of the clupeids in our waters — males average about 3 pounds and females about 4 pounds. Shad as large as 12 pounds have been reported, but one more than 6 pounds is seldom caught. This fish, like many clupeids, has compressed fusiform shape, single soft rayed back and anal fins, deeply forked tail fin, strongly serrated ventral edge of abdomen, large scales that are easily lost, and a row of dark spots behind the gill cover. A longer than deep cheek bone distinguishes it from the other fish such as Alewives or Hickory Shad with which it is frequently associated. Great difficulties are often experienced with young clupeids in discriminating between the various species.

Biology and Life History Well Known

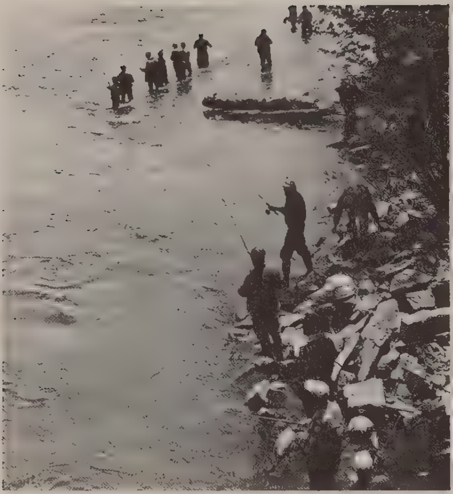
This species is anadronous, spending most of its life in the ocean but ascending coastal rivers to spawn. The spawning migrations into the Atlantic Coast rivers begin earliest in the southern part of the range (November in St. Johns River, Fla.), and are progressively later northward (June in St. John River, Canada). Those that spawn in streams south of Chesapeake Bay, and particularly south of North Carolina, apparently die after spawning. Those that spawn in streams from Chesapeake



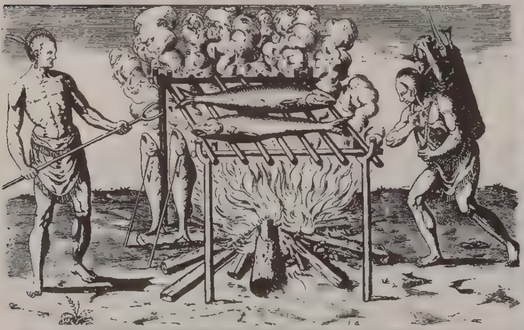
MARINE RESOURCES OF THE ATLANTIC COAST

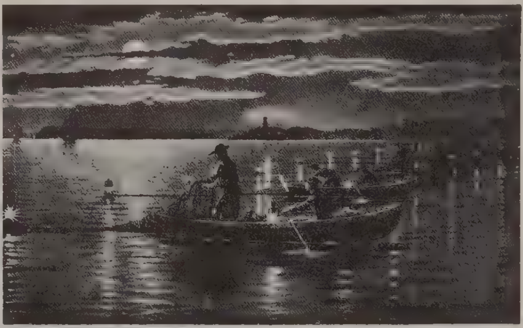
Leaflet Number 7, October 1966

ATLANTIC STATES MARINE FISHERIES COMMISSION, 336 East College Avenue, Tallahassee, Florida 32301



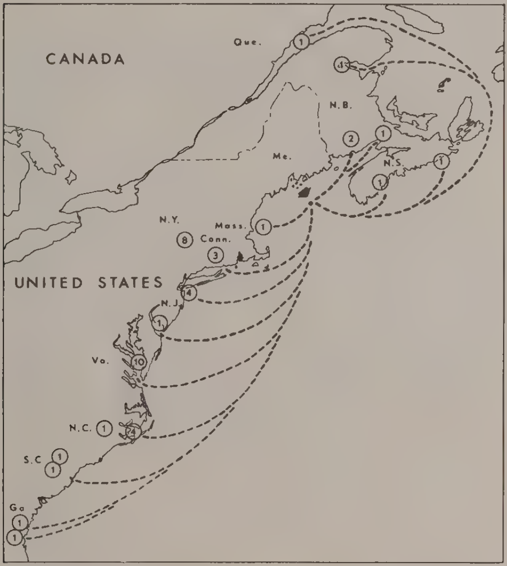
In the Connecticut River, as in many other coastal streams, Shad moving upstream pass anglers (upper left — a scene below the Enfield Dam) and are lifted across barriers (upper right — at South Hadley Falls Dam at Holyoke, Massachusetts). The two middle illustrations — from the *1896 Report of the State Commissioners of Fisheries, Pennsylvania* — show the Indian method of cooking fish and the once active Shad gill net night fishery on the Delaware River. Another scene of former years shows the results of a haul seine made by the Binghamton Shad Club in May 1905 on the upper Delaware River (lower left — photograph courtesy of Mr. Frank Bowen, Hancock, New York). Today (lower right) is much the same — pulling a Shad net on St. Johns River, Florida.



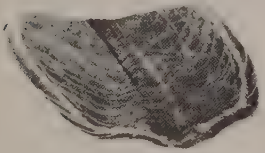


Bay to the Connecticut River migrate northward after spawning and spend the summer and autumn in the Gulf of Maine. Canadian shad also migrate southward to the Gulf of Maine and spend the summer and autumn there. The stocks scatter along the Middle Atlantic in the winter, and as the urge to spawn approaches they move inshore and then migrate either north or south to their native streams and spawn. The cycle is repeated each year the fish escape natural and fishing mortalities.

Tagged American Shad, released in the Gulf of Maine during August-September, have been recaptured in coastal bays and streams from Georgia to Quebec.



Shad mature in 2 to 5 years; males mature usually 1 year earlier than the females. The average life cycle is from 3 to 6 years, but some may live as long as 10 years. Age of the fish is determined by counting the annual growth marks on their scales, as one tells the age of a tree by counting the rings in a cross section.



Magnified projection of a Shad scale.

A female Shad deposits her eggs, from 100,000 to 600,000 depending upon her size and river of origin, in open water where fertilization takes place. The eggs hatch in 3 to 8 days (6 days at 63° F.), depending upon water temperature. The young grow rapidly in fresh water, feeding mainly on insects and crustaceans. Other fishes feed on the eggs and young.

Young Shad leave the streams in autumn when 3 to 5 inches long, probably spend the winter in the Middle Atlantic area, migrate with the adults each summer to the Gulf of Maine where they feed primarily on plankton, and when mature return to spawn in the stream where they were born. In general, the adults are comparatively free from predators other than man.

An Important Food and Game Species

Indians took Shad with bush nets, weirs, spears, and bow and arrows for summer feasts and winter forage for centuries before the white man arrived, and it is conceivable that the early settlers derived their knowledge of Shad-fishing from them. The species early became a staple item of diet because it was easily captured in large numbers and sold for as little as a penny each. The demand increased as towns and cities sprang up. Efforts were made to fish intensively to satisfy this demand for it was believed that the supply was inexhaustible. About 1850, however, the catch began to decline, and this decrease was attributed to overfishing, dams, and pollution.

In an effort to stem the early decline, the U.S. Fish Commission stocked Shad fry and eggs, and States passed stringent laws on fishing. The catch, recorded as early as 1887, increased rapidly and often exceeded 45 million pounds annually until about 1900, after which it steadily declined. Again, the decline was attributed to pollution which rendered rivers unsuitable for the species, overfishing which did not allow enough fish to spawn and replace those taken by the fisheries, and construction of dams which prevented fish from reaching spawning areas.

Today the Shad ranks 40th in relative volume and 28th in relative value of the total U.S. catch by species. The annual Atlantic Coast commercial catch is valued at about $1.5 million, with landings of about 10 million pounds. The Pacific Coast commercial harvest began at low production in 1890 of less than 1 million pounds, climbed to a high of 7 million pounds in 1915, and declined gradually until the 1960's when about 1.5 million pounds were taken annually. The Pacific Coast catch could be increased greatly, if the demand for Shad was larger.

Within the last 2 decades, the species has become highly prized as a game fish in rivers, mainly the Sacramento on the Pacific Coast, and the St. Johns, Connecticut, Delaware, and Pamlico-Tar on the Atlantic Coast. In 1964, the sport catch was about ½ million fish in more than 1 million man-days fishing — anglers in the St. Johns River caught about 125,000 shad and anglers in the Connecticut about 65,000.

Magnitude Only Change in Fisheries

The Shad is taken in the fisheries both in the rivers and along the coast by all forms of gear. The early fisheries used haul seines, weirs, stake and drift gill nets, and dip nets but the seine was the most usual and most efficient method of capture. As the fisheries progressed, the different kinds of gear were adapted to various localities. Improvements were made in techniques of fishing, with economy as an important factor. In the broad estuaries and bays, such as Delaware River and Bay, Chesapeake Bay and tributaries, and Long Island and Albemarle Sounds, mostly pound nets and long rows of stake gill nets were used. In rivers that empty directly into the ocean and generally maintain their flow characteristics to the mouth, such as the Edisto, Ogeechee, and Altamaha Rivers, extensive drift gill net fisheries developed. In most all rivers, because of their narrowness in the headwaters and concentration of fish in spawning grounds, seine, trap, gill net, and extensive bow net and rod and reel fisheries developed. In general, today's Shad fisheries have changed but little from former years except in amount of gear and size of catch.

Research and Management Productive

During the last 2 decades several States and Federal agencies, in particular Maryland, Virginia, and Connecticut, and the Bureau of Commercial Fisheries, have investigated the Shad fisheries of the Atlantic Coast, independently and jointly. The purposes of the studies were to provide basic information for improving the management of the fishery so as to arrest further decline in abundance, and make the knowledge assembled available, so that, through scientific management, the annual yield could be stabilized and probably substantially increased. In the course of the research activities many unknown facts on the life history, abundance, general biology, and factors influencing survival of the species, were made known. Through use of the knowledge assembled, several major Shad populations are now being managed more effectively.

The most effective management procedures involve providing safe passage where the species are blocked from spawning grounds; abating pollution so that fish will survive better and regulating the fisheries by such measures as closed days to reduce fishing effort and limiting the number of fishermen and kinds, amounts, and size of gear to allow more fish to reach the spawning area. So many different regulations govern the fisheries along the coast that local State agencies should be consulted for details. The fisheries in each river are regulated by State and county statute.

Problems, Research and Restoration

Prospects for maintaining productive Shad fisheries and increasing supplies of the species, depend upon reducing pollution, establishing appropriate regulations, minimizing adverse effects of water development on spawning and nursery grounds; and providing fish passage facilities at proposed and existing dams, especially the latter two. Attempts to propagate Shad by means of hatcheries have never been successful, as operated, in increasing natural reproduction. An accelerated pace of water developments for navigation, power, and flood control are making enormous changes in rivers, and Shad are faced with problems that threaten their existence. By rule of thumb "the size of run will be reduced in proportion to the amount of spawning area eliminated, and vice versa". Together with State and Federal agencies the Bureau of Commercial Fisheries is studying whether runs of Shad can be restored in rivers above dams if navigation locks are practical for upstream passage of anadromous fish, whether fish lifts and pool-type fishways are effective for restoring runs of Shad above dams, and what, if any, effects do proposed flood control projects have on the Shad fisheries. Not until we obtain solutions to the problems encountered by the Shad, will we be able to protect and conserve this valuable resource. If the annual yield could be restored to historic levels, it would bring a return to commercial fishermen, at today's prices, of more than $6.5 million, and provide untold number of man-days fishing to anglers.

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STRIPED BASS

"The Basse is one of the best fishes in the country . . . the way to catch them is with hooke and line: the Fisherman taking a great codline, to which he fasteneth a piece of Lobster, and throws it into the sea, the fish biting at it he pulls her to him, and knocks her on the head with a sticke . . . the English at the top of an high water doe crosse the creeks with long seanes or Basse netts, which stop in the fish; and the water ebbing from them they are left on dry ground, sometimes two or three thousand at a set . . ."

From William Wood, New England's Prospect (1635)

This fish, of the sea bass family Serranidae, with scientific name *Roccus saxatilis* (Walbaum) and common name "Striped Bass" and "Rock" or "Rockfish," is still one of the most valuable anadromous fishes on the coasts of North America. Although the species is distributed from the St. Lawrence River, Canada, to St. Johns River, Fla., and in tributary streams of the Gulf of Mexico from western Florida to Louisiana on the Atlantic Coast, it is most abundant in Chesapeake Bay. In 1879 and 1881, a number of yearling fish were seined in New Jersey, taken across the continent in tanks by train, and planted in San Francisco Bay, where they prospered and now occur from southern California to Washington. A landlocked population was established with the impounding of Santee-Cooper Reservoir in South Carolina; however, attempts to establish the species in other fresh-water impoundments have had only limited success.

Its high-quality, white, flaky flesh is in high demand as a food, and a substantial commercial fishery has existed since colonial days. At the same time, its voracious predatory feeding habits places it in high demand as a game fish that is avidly sought by a large and growing group of anglers.

Easily Recognized

Striped Bass more than 4 inches long would hardly be confused with any other species on the Atlantic or Pacific Coasts; however, where introduced into Mississippi and Ohio Valleys, it could be confused with the fresh-water species of Yellow Bass and White Bass, *Roccus mississippiensis* and *R. chrysops*. Its prominent dark longitudinal stripes, general outline, and fin structure are sufficient to separate it at a glance from other species. The seven or eight dark stripes, much the same olive-green color as the back, usually parallel the rows of scales three or four above the lateral line, one invariably on the lateral line, and three below it. Dorsal fins are clearly separate, not touching at the base. The body is elongate and little compressed, with the contour of the back little arched.

Historically Important

Striped Bass ranks close to the immortal Codfish in the vital part which our fishery resources played in early American history. Together, they were probably the first natural resources in colonial America subject to conservation measures enacted by statute — the General Court of Massachusetts Bay Colony in 1639 ordered that neither fish should be used as fertilizer for farm crops. The first public (free) school of the New World was made possible through monies derived, in part, from the sale of Striped Bass. A portion of the monies was also expended in helping widows and orphans of men formerly engaged in service to the Colony.

Early Decline in Abundance

Early settlers in New England were astonished by the abundance of this fish. Abundant as it may have seemed, however, its ease of capture made possible a

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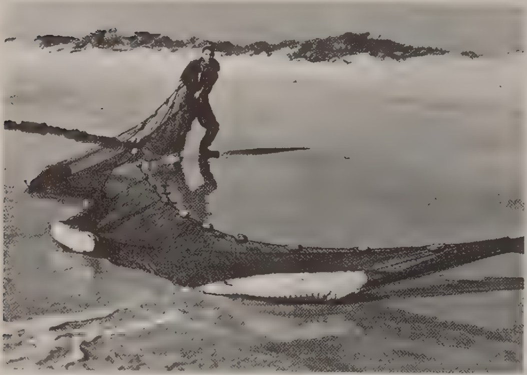
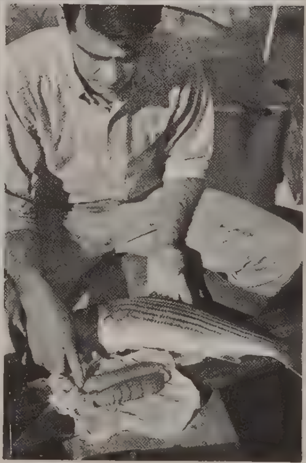
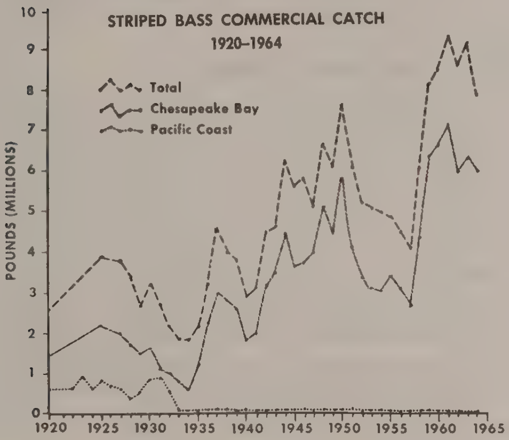
ATLANTIC STATES MARINE FISHERIES COMMISSION, 336 East College Avenue, Tallahassee, Florida 32301

Commercial fishermen in North Carolina drifting a gill net for Striped Bass in the Roanoke River (upper left) and unloading a catch from Albemarle Sound (upper right). A series of three scenes (middle left and right, lower center) shows biologists beaching a haul seine on the Outer Banks of North Carolina and moving jumbo specimens for measuring and tagging. Other biological data are obtained from length and weight measurements — on specimens sampled from the gill net fishery in Chesapeake Bay, Maryland (lower left) — and by stripping the ovaries for a fecundity study (lower right).





decrease in supply over its northerly range. Although overfishing was probably the initial cause of this decline, construction of dams blocking access to spawning grounds and pollution in rivers played effective parts in the decrease of this species, as well as other anadromous food fish such as American Shad, Atlantic Salmon, and Sturgeon. A decline in the supply of Striped Bass in Chesapeake Bay was not as marked as in more northerly areas, probably because the bay had less industrial development and more limited population than the north. Nevertheless, smallest catches were noted in many sections of its more southerly range.



Commercial Harvest is High

The supply of this fish has varied widely during the past 50 years and probably since its fishery began. Unfortunately, accurate catch records, which are the only means of estimating relative abundance in different periods, are not available for early years. Fortunately, the stocks have been high in recent years, and have supported large food and sport fisheries.

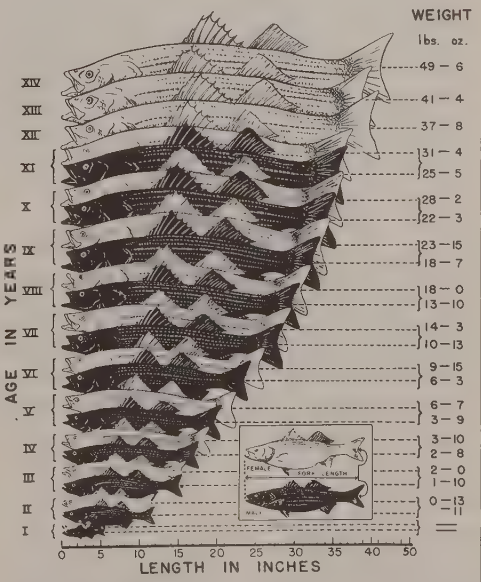
The commercial harvest along the Atlantic Coast has been increasing, with minor fluctuations, during the past 3 decades. Today the annual commercial catch is more than 8 million pounds worth about $1.5 million. Commercial fishing is geared mainly for 2- and 3-year-old fish, weighing from 1 to 2 pounds. Specimens over 60 pounds are seldom encountered; however, the record size is 125 pounds. Various gears used in the fishery include haul seines that take about 20 percent of the catch, pound nets 25 percent, gill nets 50 percent, fyke nets and miscellaneous gears 5 percent. Since 1963, the otter trawl winter fishery along the New Jersey coast has made substantial catches.

On the Pacific Coast, the supply of Striped Bass has increased many fold since its introduction. Prior to 1930, the commercial fishery yielded over 17 million pounds. In 1931, California declared it a sport species, and commercial netting was prohibited.

Recreational Use Important and Growing

Early historians noted that angling for Striped Bass was almost unexcelled and identified the species as the "boldest, bravest, strongest, and most active fish that visited tidal waters and bays along the Atlantic seaboard." Even today, its value to many areas is greater from a recreational than from a food standpoint. The sport catch is substantial but unrecorded, except in isolated instances. The U. S. Fish and Wildlife Service reports that sports fishermen took more than 9 million Striped Bass in tidal waters along the Atlantic coast in 1960. On the Pacific coast, the average annual catch is about 3 million fish, of which California produces more than 2 million. In Chesapeake Bay, the sport catch is about equal to the commercial catch. The sport catch is made by all types of fishermen from the highly specialized spin caster and troller to the less skilled but eager bait angler. From southern New Jersey to Cape Cod it is the unchallenged first choice of surfcasters.

AVERAGE LENGTH AND WEIGHT OF STRIPED BASS, *Roccus saxatilis*, AT DIFFERENT AGES



Biology Well Known

The species is anadromous, that is, it ascends rivers from March to July to spawn and may go upstream as far as 200 miles from salt water. During the spawning act, a single large female is surrounded by a few to many males. Spectacular "fights" then ensue, which are really courtship antics, and are accompanied by deposition of eggs. The number of eggs produced by each female varies with size: 14,000 by a 3-pounder female and nearly 5 million by a 50-pounder. The eggs hatch in about 2 days at a water temperature of 65° F. The young range in length from 3 to 6 inches at the end of the first year.

Striped Bass are voracious and carnivorous — they feed mostly on other fishes, but also take considerable quantities of invertebrates, especially crustaceans.

Females reach maturity in 4 or 5 years, at which time they weigh from 4 to 5 pounds. Most males are mature when 2 years old and all are mature at 3 years. The fish grow rapidly early in their life, but an increase in weight and length tapers off after the 10th year. The age of the fish is determined by counting the annual growth marks on their scales, as one tells the age of a tree by counting the rings in a cross section.

Striped Bass travel in large schools, especially after they are 2 years old. Tagging studies have shown that the fish are relatively inactive during the winter and congregate in deep pools near the river mouths and in bays and estuaries. In the spring, mature fish move into rivers and on upstream to spawn.

After spawning the mature fish move out of the rivers into open water for feeding through summer and fall. Certain segments of the Atlantic Coast stocks, primarily from the Hudson River and Chesapeake and Delaware Bays, leave their native areas and make coastal migrations. They move northward in late winter or early spring and congregate off the New England coast. These migrants remain in the New England area until autumn, when they move southward to their "home" area. There is evidence that Striped Bass return to their native stream to spawn.

Research and Management Essential

Effective management can only be built upon a thorough understanding of the biology of the Striped Bass and knowledge of the fisheries. Most States throughout the range of the species and the Fish and Wildlife Service are studying its life history, migration patterns, size of stocks, and causes of fluctuations in abundance. Management measures, based on such research, have been initiated by the States in an effort to use the resource more effectively. These include: minimum and maximum size limits, daily bag limits, control of the amount and type of gear and season of fishing, and pollution abatement. Attempts to propagate Striped Bass by means of hatcheries have never been successful, as operated, in increasing natural reproduction. Hatcheries for the species are in operation on the Roanoke River at Weldon, N. C., and Santee-Cooper River at Moncks Corner, S. C. Because there are a number of different management policies governing fishing, local State agencies should be consulted for details.

Wiser Management Possible

The present fisheries for Striped Bass are productive and essentially healthy; however, continuation of research is necessary to make available additional biological information on which to build a more effective management policy. The major problems now are changes in the environment resulting from water developments for hydroelectric power, navigation, and flood storage; increased domestic and industrial pollution entering rivers; and increased competition between sport and commercial fishermen. Striped Bass, as with other fishes, must be given an opportunity to survive. Wiser management toward conserving the species for the future is possible, but only through the coordinated efforts of local governments and society.

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AN ESTIMATE OF TOTAL CATCH AND EFFORT OF THE JAPANESE LONGLINE FISHERY IN THE PACIFIC OCEAN, 1953-63

By

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ABSTRACT

The Japanese longline fleet fishes for tunas in the Atlantic, Indian, and Pacific Oceans. Before 1962, published statistics did not separate the catches by areas, even as broadly as by oceans. Similarly, information on total effort was not available. The total Pacific longline catch and effort are estimated in this paper. Estimates of the contribution of the Pacific Ocean to the total Japanese catch ranged from almost 100 percent (1953) to about 63 percent (1963). The estimated total longline effort in the Pacific Ocean ranged from 59.2 million hooks in 1953 to a high of 270.9 million in 1962, and declined to 220.2 million in 1963.

INTRODUCTION

Until 1962, published data on the Japanese catch of tunas and billfishes were classified primarily by method of fishing and did not always specify the area. As a result, the total Japanese longline catch and effort in any area--even one so large and productive as the Pacific Ocean--have never been definitively established. We have attempted crude estimates from the available data, following the procedures described below. They are presented here in the absence of more reliable information.

ESTIMATION OF CATCH

Total Japanese longline catch, by species, was obtained from the Annual Report of Catch Statistics of Fishery and Aquiculture (published by the Ministry of Agriculture and Forestry, Government of Japan). To separate these landings into catches made in the Pacific, Indian, or Atlantic Oceans, some manner of estimation was necessary. Estimates for different years were made as follows, on the basis of information on the history of the Japanese longline fishery, not necessarily documented; the percentages are gross approximations.

1953 and 1954.--That portion of the total longline catch by species from the *Annual Report of Catch Statistics on Fishery and Aquiculture* not classified by area was divided, 98 percent being attributed to the Pacific Ocean and 2 percent to the Indian Ocean. No Atlantic Ocean catches were made.

1955.--Total longline catch by species from the *Annual Report* was divided--95 percent was attributed to the Pacific Ocean and 5 percent to the Indian Ocean. No catches were made in the Atlantic Ocean.

1956.--Total longline catch by species from the *Annual Report* not classified by

Table 1.--Estimated total Japanese longline catch by species and ocean, 1953-63 (in 1,000 metric tons)

Year	Ocean	Total	Species						
			Yellowfin tuna	Bigeye tuna	Albacore	Bluefin tuna	Striped marlin	Broadbill	Blue and black marlin
1953	PACIFIC	104.2	28.5	25.5	18.5	5.8	2.9	7.4	15.6
	Indian	2.0	0.5	0.5	0.4	0.1	0.1	0.1	0.3
	Total	106.2	29.0	26.0	18.9	5.9	3.0	7.5	15.9
1954	PACIFIC	131.5	42.2	22.6	26.8	4.6	8.7	8.9	17.7
	Indian	2.4	0.8	0.4	0.5	0.1	0.1	0.2	0.3
	Total	133.9	43.0	23.0	27.3	4.7	8.8	9.1	18.0
1955	PACIFIC	158.1	57.2	35.9	23.2	3.9	5.9	11.8	20.2
	Indian	7.3	2.7	1.8	0.8	0.2	0.2	0.6	1.0
	Total	165.4	59.9	37.7	24.0	4.1	6.1	12.4	21.2
1956	PACIFIC	178.4	68.1	39.6	21.3	8.5	6.5	12.3	22.1
	Indian	36.0	14.3	8.3	3.2	1.9	1.2	2.4	4.7
	Total	214.4	82.4	47.9	24.5	10.4	7.7	14.7	26.8
1957	PACIFIC	192.1	71.3	43.9	24.4	11.8	5.4	9.8	25.5
	Indian	30.2	11.4	7.3	2.8	2.1	0.9	1.5	4.2
	Atlantic	15.8	13.2	0.4	0.9	0.1	-	1.2	-
	Total	238.1	95.9	51.6	28.1	14.0	6.3	12.5	29.7
1958	PACIFIC	216.2	66.8	58.4	35.3	11.0	8.2	12.5	24.0
	Indian	33.1	10.4	9.9	3.6	1.9	1.3	1.9	4.1
	Atlantic	30.6	27.2	0.5	2.0	-	0.1	-	0.8
	Total	279.9	104.4	68.8	40.9	12.9	9.6	14.4	28.9
1959	PACIFIC	248.1	62.5	60.5	45.3	37.5	8.3	11.5	22.5
	Indian	38.5	10.6	10.4	4.9	5.5	1.4	2.0	3.7
	Atlantic	50.5	44.1	1.5	3.6	0.3	0.1	0.1	0.8
	Total	337.1	117.2	72.4	53.8	43.3	9.8	13.6	27.0
1960	PACIFIC	274.1	79.7	57.9	49.9	46.3	7.5	12.2	20.6
	Indian	43.4	12.9	10.2	5.5	8.1	1.2	2.1	3.4
	Atlantic	71.7	57.8	2.8	8.5	0.7	0.1	0.3	1.5
	Total	389.2	150.4	70.9	63.9	55.1	8.8	14.6	25.5
1961	PACIFIC	307.5	76.2	85.5	52.3	50.0	8.2	12.9	22.4
	Indian	48.8	12.7	15.4	4.9	8.8	1.2	2.2	3.6
	Atlantic	83.7	53.9	11.3	13.0	1.4	0.6	0.7	2.8
	Total	440.0	142.8	112.2	70.2	60.2	10.0	15.8	28.8
1962	PACIFIC	327.0	86.5	91.7	65.6	28.1	13.5	15.5	26.1
	Indian	66.4	21.2	18.9	10.2	5.2	2.5	2.9	5.5
	Atlantic	82.6	38.4	14.6	20.0	3.4	1.4	0.3	4.5
	Total	476.0	146.1	125.2	95.8	36.7	17.4	18.7	36.1
1963	PACIFIC	271.9	60.7	98.3	43.6	16.8	13.2	16.1	23.2
	Indian	88.9	26.7	15.2	15.6	23.2	2.2	1.0	5.0
	Atlantic	101.8	37.7	14.5	29.7	7.8	2.4	1.1	8.6
	Total	462.6	125.1	128.0	88.9	47.8	17.8	18.2	36.8

area was divided, 80 percent being attributed to the Pacific Ocean and 20 percent to the Indian Ocean. No Atlantic Ocean catches were made.

1957 through 1962.--That portion of the total longline catch by species from the Annual Report not classified by area was divided, 85 percent being attributed to the Pacific Ocean and 15 percent to the Indian Ocean.

1963.--Total longline catches by species and by ocean were taken directly from the English edition of Fishery Statistics of Japan-1963, Ministry of Agriculture and Forestry, Government of Japan.

The estimates made in this manner appear in table 1.

ESTIMATION OF EFFORT

Data published on total effort in the Annual Report of Catch Statistics of Fishery and Aquiculture are in terms of the number of vessels. No records are given on the number of days or the number of hooks fished. Effort data appearing in Tuna Fishing (published monthly by the All Japan Investigative Conference of Tuna, Misaki Branch, c/o Kanagawa Prefectural Fisheries Experimental Station, Misaki-machi, Miura-shi, Kanagawa, Japan) are presented in terms of the number of hooks fished, but represent only a variable portion of the total Japanese fishing effort. To obtain an estimate of total Japanese longline effort in the Pacific in terms of the number of hooks fished, both sources of data were utilized.

To estimate the proportion of the Japanese tuna catch in the Pacific that is documented in Tuna Fishing, we: (1) took the catch in numbers of yellowfin and bigeye tuna and albacore as given in the issues of that journal for the years 1953-63; (2) converted them to thousands of metric tons to give us weights comparable with those in table 1; (3) summed these weights for all three species for each year; and (4) divided them into the estimated totals for these species for each year from

Table 2.--Calculation table for total Japanese Pacific longline effort in terms of number of hooks. (Weights for the number of fish reported in Tuna Fishing were obtained by assuming the average weight of yellowfin tuna as 90 pounds, bigeye tuna as 100 pounds, and albacore as 50 pounds)

Year	Catch reported in Tuna Fishing						A	B	C	D	E
	Yellowfin		Bigeye		Albacore		Total catch of yellowfin, bigeye, and albacore from Tuna Fishing (1,000 metric tons)	Total catch of yellowfin, bigeye, and albacore (table 1 (1,000 metric tons)		No. hooks fished Tuna Fishing (millions)	D/C = estimated total hooks fished in Pacific (millions)
	No. (1,000)	Wt. (1,000 metric tons)	No. (1,000)	Wt. (1,000 metric tons)	No. (1,000)	Wt. (1,000 metric tons)			A/B		
1953	257.7	10.5	187.3	8.5	319.9	7.3	26.3	72.5	0.363	21.5	59.2
1954	478.3	19.6	231.0	10.5	916.6	20.8	50.9	91.6	0.556	45.6	82.0
1955	354.1	14.5	300.6	13.7	322.6	7.3	35.5	116.3	0.305	34.4	112.8
1956	301.6	12.3	225.9	10.3	177.0	4.0	26.6	129.0	0.206	24.3	118.0
1957	512.4	21.0	343.5	15.6	270.5	6.1	42.7	139.6	0.306	31.0	101.3
1958	633.9	25.9	594.2	27.0	447.2	10.2	63.1	160.5	0.393	50.2	127.7
1959	578.0	23.6	504.5	22.9	350.8	8.0	54.5	168.3	0.324	54.1	167.0
1960	-	-	-	-	-	-	-	-	-	-	-
1961	496.6	20.3	493.1	22.4	329.6	7.5	50.2	214.0	0.235	51.5	219.1
1962	513.7	21.0	601.7	27.4	525.2	11.9	60.3	243.8	0.247	66.9	270.9
1963	427.5	17.5	491.1	22.3	373.9	8.5	48.3	202.6	0.238	52.4	220.2

table 1. This procedure gave us ratios between the catch as shown in Tuna Fishing and that estimated from the Annual Reports. We then applied this ratio to the number of hooks given in Tuna Fishing to obtain an estimate of total effort in the Pacific. For example, in 1963 an estimated 0.238 of the total Pacific effort was 52.4 million hooks. The total Pacific effort thus was 220.2 million hooks. Data required for this calculation and the estimates of total Japanese longline effort in the Pacific are presented in table 2.

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Improved Destaining Tube for Use in Disk Electrophoresis

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The destaining procedure in polyacrylamide disk electrophoresis with the Canalco Model 12 assembly often presents a problem of securing a seal at the bottom of the stain-destain tube tight enough to prevent excessive leakage of solution from the upper to the lower bath. It has been found that this problem can be obviated by the preparation of a separate set of tubes and their use with disks of membrane filter cut to proper size.

Fabrication. Section 8-mm. glass tubing into 6.5-cm. lengths and evenly grind or fire polish the ends. Cut disks approximately 1 cm. in diam. from membrane filter of 0.45-μ porosity using a No. 7 cork borer. Coat one end of each length of tubing with clear nail polish, press onto a disk, and allow to dry. Place a polyacrylamide gel column in such a tube, carry out the destaining procedure in the usual manner, and remove the disk.

The gel is properly destained while the excess of stain readily permeates the membrane filter. After completion of the run, the filter disk can be removed easily without disturbing the column.

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Small-scale, Horizontal Vortices in the Surface Layer of the Sea

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Small-scale, Horizontal Vortices in the Surface Layer of the Sea[1]

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ABSTRACT

A vortex system in the water near the sea surface has been inferred from collection into parallel rows of a positively phototaxic zooplankton population. Water velocity in the upper part of convergence planes of the system has been equated with estimated swimming speed of the animals.

A thermohaline driving force was inferred to have produced the circulation system, and the depths to which the vortices extended were derived from heat-flux observations. The computed depth of 61 cm is close to the predicted depth of 64 cm.

Introduction. This paper describes a vortex system encountered at sea. Meteorological conditions and the small scale of the circulation suggest that it was a consequence of thermal energy exchange across the sea surface. Vertical velocity in the circulation has been estimated by observing the swimming rate of a zooplankter, and the depth to which the circulation extended has been derived from meteorological and oceanographic observations.

The accumulation of materials in parallel rows at the sea surface often has been attributed to their concentration at convergence lines of horizontal, parallel vortices (e.g., Bainbridge 1957, Sutcliffe et al. 1963, Faller and Woodcock 1964). Two general mechanisms have been proposed for vortical cell generation in the surface layers of the sea: Langmuir (1938) and subsequent authors attributed rows of foam, leaves, and the buoyant alga *Sargassum* to their collection along convergence lines of wind-generated vortices, whereas Montgomery et al. (1947) examined the nature of cells in free convection, driven by thermal energy exchange. To date, no specific mechanism has been proposed to account for vortical cell generation by wind, nor has an observational study been made that distinguishes between the two modes of generation.

Suspension of a particle near the surface in a convergence plane requires that the intrinsic ability of the particle to move upward (by positive buoyancy

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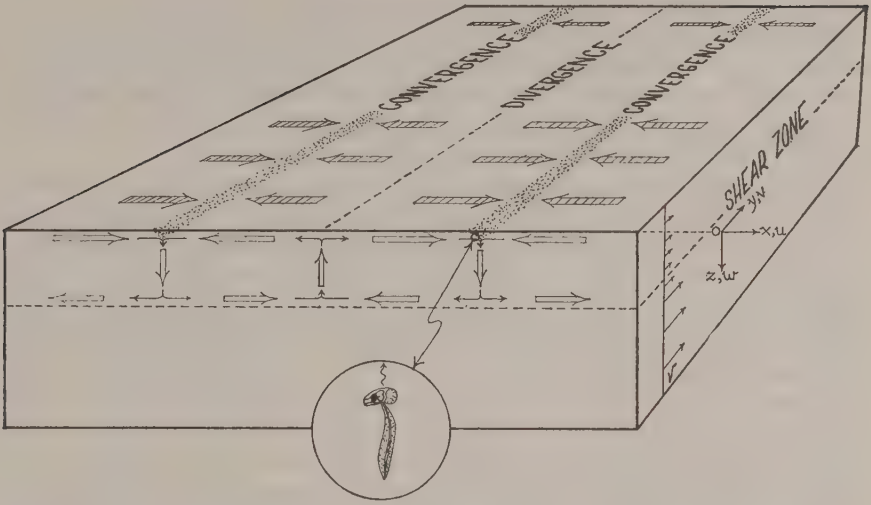

Figure 1. Water motion in the x, z plane of a vortex system and the resulting distribution of upward-moving particles introduced at the system boundaries. The selection of $\partial v/\partial z > 0$ is arbitrary.

or upward swimming) be greater than the extrinsic tendency to its downward transport by the drag of the surrounding fluid. All such particles in the region of a vortex system will of necessity collect near the surface along convergence sites (Fig. 1). By contrast, to concentrate particles near the surface along convergences requires that the particles only possess this intrinsic tendency, no matter how small their upward movement relative to the fluid may be. In the case where the intrinsic tendency is small and the particle velocity is close to the fluid velocity, particles are nowhere stationary and are present elsewhere in the vortex as well as at the convergence site.

The vertical component of water velocity, w, is zero at the upper and lower limits of a vortex system. Between these limits, in each of the convergence planes, w attains a single maximum. If a nonbuoyant plankton population is found in these convergence planes and is absent elsewhere in the system, then its members are presumably swimming up at the same speed as the downward flow at their depth in the plane. Further, if w may be said to approach its maximum value within a short distance, δ, of the sea surface, then the swimming speed of members of the above population that are located at $z > \delta$ must numerically equal the maximum value of w in the vortices.

Observations. Rows of dense reddish concentrations of zooplankton organisms, consisting mainly of *Oikopleura longicauda* (Vogt), were observed during calm weather from an oceanographic vessel about 180 nautical miles (335 km) off the California coast. The rows were observed for a distance of about 40 nautical miles (74 km) and initially were approximately normal to the ship's course of 102°T. Breadth of individual rows varied from 2 to 8 cm, and their depth appeared to extend to 5 cm. Meanders, offshoots, and bifurcations were seen but, in general, rows were straight and parallel for distances in excess of 30 m. Distance between rows was nearly constant at 1.5 m.

Samples of water from a row were obtained with a plastic bucket.[1] Behavior of the oikopleurans in the bucket first was observed under direct sunlight and then in a dim, diffusely lighted shipboard laboratory. Positive phototaxis was inferred from the difference in behavior of the animals under these two conditions; in direct sunlight, the animals moved quickly to the water-air interface, but in the laboratory they remained well dispersed by depth although a few individuals collected at the surface after about five minutes. No tendency of the animals to collect in clumps or patches in the bucket was observed under either direct or diffuse lighting.

Mean swimming rate of the oikopleurans was estimated under direct sunlight by measurement of the time required for animals in a gently mixed sample to reach the water-air surface. After most of the water motion stopped, animals still appeared to be well distributed through the 25-cm depth of water in the bucket. Their ascent appeared to proceed at a uniform rate; no animal was seen to pass or lag behind others. In two minutes, 13 to 15 *Oikopleura* were seen just below the 0.5-cm surface layer; the remaining ones, about 85, were within this layer. If we assume (i) initial uniform dispersion of animals throughout the water depth, and (ii) no large-scale vertical water motion in bucket, at least five of the 20 *Oikopleura* present initially in the lowest 5 cm of the bucket arrived in the surface layer within two minutes; hence each of these five animals swam at an average rate of at least 0.2 cm sec^{-1}. Furthermore, the uniform swimming speed indicated that the 13 to 15 *Oikopleura* seen just below the 0.5-cm surface layer after two minutes had in fact begun their trip from the lowest 5 cm of the bucket. Therefore, each of these swam at an average rate of less than 0.2 cm sec^{-1} but more than 0.16 cm sec^{-1}. The best estimate of swimming speed of this isolated population thus appears to be 0.2 cm sec^{-1}.

Selected oceanographic and meteorological observations made on June 16, 1964, the day the rows were observed, are summarized in Table I. For comparison, data taken the day before and the day after observation of the rows are included. The ship was underway between oceanographic and meteorological observations, and therefore the data must be regarded in terms of space as well as time. Bathythermograms provided the main source of subsurface data.

Wind speed, which was essentially zero at the ship for 24 hours before rows were sighted at 1230 PST, June 16, increased shortly thereafter. Greater

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[1] Samples collected at 1540 PST, June 16, 1964, 33°48′N, 124°45′W, from R/V Black Douglas of the U.S Bureau of Commercial Fisheries.

Table I. Oceanographic and meteorological conditions at the ship on June 15–17, 1964. The quantity $\Delta_z\vartheta$ measures extent of the transient thermal structure (see text), D_p is the mixed-layer depth, and p is barometric pressure. Air observations made at 6 m above sea surface. Barometric pressure adjusted to sea level.

			Air					Sea		
Time-Date PST	Lat. N.	Long. W.	Cloud cover fraction	Wind force Beaufort	Dry bulb ϑ °C	Wet bulb ϑ °C	p mb	ϑ_o °C	$\Delta_z\vartheta$ °C	D_p m
0600–15	34°33′	129°09′	0.8	0	15.6	15.3	1019	15.7	0.0	38
0900–15	34°29′	128°53′	0.8	2	15.5	14.6	1019	16.2	0.4	35
1210–15	34°25′	128°29′	0.8	0	16.4	14.0	1019	16.0	0.1	–
1500–15	34°20′	128°05′	0.3	0	18.3	15.3	1018	18.3	2.3	33
1800–15	34°20′	127°44′	0.7	0	17.5	15.3	1018	19.3	3.2	35
2055–15	34°15′	127°19′	0.7	1	16.7	14.4	1018	17.2	1.0	32
2330–15	34°10′	126°50′	0.8	0	16.6	13.7	1018	16.5	0.4	38
0200–16	34°05′	126°23′	0.7	1	15.8	13.7	1017	16.1	0.0	42
0630–16	34°00′	125°56′	0.8	0	15.3	13.9	1018	15.7	0.0	35
1015–16	33°54′	125°32′	0.6	0	17.8	15.6	1018	16.2	0.3	36
1400–16	33°51′	125°01′	0.2	2	16.1	13.3	1018	16.7	2.2	38
1730–16	33°46′	124°28′	0.3	3	16.0	14.0	1018	15.6	1.2	35
1930–16	33°42′	124°16′	0.2	2	15.3	13.4	1018	15.3	0.5	(30)
2320–16	33°37′	123°38′	0.3	4	15.0	13.4	1018	16.1	0.1	33
0230–17	33°32′	123°18′	0.2	4	15.8	13.9	1017	15.8	0.0	30
0600–17	33°25′	122°40′	0.0	4	15.3	13.9	1017	14.3	0.0	(50)
1000–17	33°21′	122°16′	0.8	5	15.6	14.2	1019	14.3	0.1	(32)
1500–17	33°07′	121°32′	0.7	4	16.7	15.3	1017	14.9	0.2	44
1800–17	33°02′	121°02′	0.7	5	15.4	13.5	1016	14.4	0.1	40

irregularities in individual rows accompanied the increase in wind speed, but rows persisted at least until sunset on the 16th.

During the day, a near-surface transient thermal discontinuity was encountered. The thermal magnitude of the discontinuity was estimated by the difference ($\Delta_z\vartheta$) between sea-surface temperature (ϑ_o) and the zero-depth temperature extrapolated from bathythermograms (see insert on Fig. 2). Therefore, the quantity $\Delta_z\vartheta$ is the difference between the sea-surface temperature observed and that to be expected if no transient structure had developed. Data in Fig. 2, depicting diurnal development and decay of the transient near-surface thermal structure, suggest that the structure was not some steady-state phenomenon. These data permit development of the transient thermal structure on a nearly calm day to be compared with its development on a windy day.

The depth of the transient thermocline could not be measured from bathythermograms with sufficient accuracy to determine heat exchange across the sea surface; consequently, this exchange was estimated from the meteorological observations. Incoming solar radiation was monitored with a 10-junction Eppley pyranometer; the resulting insolation curve was integrated with respect

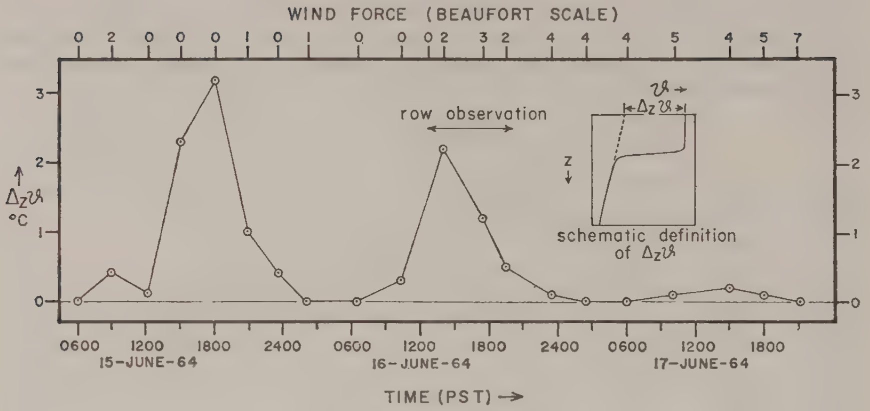

Figure 2. Development and decay of transient thermal structure, June 15–17, 1964. Points represent BT observations.

to time, and a reflectance correction was applied to express Q_r, net short-wave radiation penetrating the sea surface. Corrections for reflectance were obtained from Sverdrup et al. (1942: table 26) and were applied in the form

$$Q_r = Q_t(1 - \bar{r}),$$

where Q_t is the recorded direct and diffuse insolation rate and $\bar{r}$ is the average reflectance over the integration period.

Effective back-radiation rate, the difference between rates of long-wave radiation from the sea surface and long-wave radiation from the atmosphere, was computed from the formula reported by Budyko (1956: 46):

$$Q_b = s\sigma T_a^4(0.39 - 0.058[e_s]^{1/2})(1 - kC^2) + 4s\sigma T_a^3(T_s - T_a),$$

where the following definitions obtain:

s,	ratio of emittance of sea surface to that of a black-body = 0.97;
σ,	Stefan-Boltzmann constant = 7.888×10^{-11} cal cm^{-2} °K^{-4}min^{-1};
T_s, T_a,	absolute temperature of sea, air, °K;
e_s,	saturation vapor pressure at sea surface corrected for salinity effect, mb;
k,	function of vertical development and base height of clouds, here = 0.64;
C,	fraction of sky covered by clouds.

Heat-exchange rate by evaporation, Q_e, was computed from an expression adapted from Montgomery (1940):

$$Q_e = L_\vartheta E = L_\vartheta \varrho_a \varkappa_0^2 \Gamma_E^2 \left(0.623 \frac{\Delta e}{p}\right) \bar{U}_a ,$$

where the following definitions obtain:

L_ϑ,	latent heat of evaporation $= 596 - 0.52\,\vartheta$ cal $\text{gm}^{-1}\,{}^\circ\text{C}^{-1}$;
E,	evaporation, gm $\text{cm}^{-2}\text{min}^{-1}$;
ϱ_a,	air density $= 1.2 \times 10^{-3}$ gm cm^{-3};
$\varkappa_0$,	Karman constant $= 0.4$;
Γ_E,	coefficient for expression of humidity gradient evaluated from Deacon and Webb (1962: fig. 17); at low wind-speed values $= 0.1$, and at higher wind speeds encountered (> 2 Beaufort) $\doteq 0.085$;
$\Delta e = e_s - e_a$,	vapor pressure at sea surface and height a (ca. 6 m), respectively [$0.623\,(\Delta e/p) = \Delta q$, specific humidity gradient];
p,	barometric pressure at sea surface, mb;
$\bar{U}_a$,	wind speed at height a (ca. 6 m), cm sec^{-1}.

Conductive heat-exchange rate, Q_c, was computed from the evaporative exchange rate by the Bowen ratio, R (Bowen 1926):

$$Q_c = R Q_e ,$$

where $R = 0.66 \times 10^{-3} p\ (\Delta\vartheta/\Delta e)$, ($\Delta\vartheta = \vartheta_0 - \vartheta_a$, sea temperature less air temperature, °C).

The net heat-exchange rate across the sea surface due to the above processes is then

$$Q_\Sigma = Q_r + Q_b + Q_e + Q_c , \tag{1}$$

wherein the positive sense denotes heat gained by the sea. Computed values for each term above are presented in Table II.

Probable Causes of Row Formation. Two mechanisms other than convergent flow between cells may produce parallel rows of particles at the sea surface. Roughly isometric patches of plankton, formed initially at the sea surface by behavioral mechanisms, may be drawn out into rows in the presence of current shear. This possibility is discounted in the situation described here, since observed row spacing was nearly constant—not an expected result of this mechanism. Bary (1953) suggested that some organisms may be aggregated at the surface in slicks formed by internal waves. Narrow rows of organisms were observed, however, whereas broad rows would be expected in this circumstance. Furthermore, characteristic wave lengths of 1.5 m are too short for standing internal waves.

Since wind speed was zero when the rows were sighted, the phenomenon was not the wind-driven Langmuir circulation. Furthermore, it is not likely

Table II. Heat budget in cal cm^{-2} min^{-1} on June 15–17, 1964 in the vicinity of 33°45′N, 124°30′W. Positive quantities denote heat gained by sea, negative quantities denote heat lost by sea. Symbols explained in text.

Time-Date PST	Q_r^*	Q_b	Q_e	Q_c	Q_Σ
0600–15	0.030	−0.049	0	0	−0.019
0900–15	0.518	−0.053	−0.007	0.003	0.461
1210–15	1.048	−0.046	−0.005	−0.002	0.995
1500–15	0.960	−0.071	−0.007	0	0.882
1800–15	0.115	−0.062	−0.022	0.008	0.039
2055–15	0	−0.057	−0.012	0.002	−0.067
2330–15	0	−0.048	−0.010	−0.004	−0.062
0200–16	0	−0.054	−0.009	0.001	−0.062
0630–16	0.066	−0.051	−0.016	−0.002	−0.003
1015–16	1.067	−0.049	−0.008	0.007	1.017
1400–16	1.183	−0.081	−0.033	−0.003	1.066
1730–16	0.324	−0.074	−0.017	0.002	0.235
1930–16	0	−0.080	−0.024	−0.001	−0.105
2320–16	0	−0.085	−0.017	−0.003	−0.105
0230–17	0	−0.080	−0.020	0	−0.100
0600–17	0.141	−0.072	0.009	−0.014	0.064
1000–17	0.660	−0.042	0.019	−0.024	0.613
1500–17	0.687	−0.047	0.029	−0.025	0.644
1800–17	0.174	−0.053	0.004	−0.018	0.107

* By integration of insolation curve over one-hour period around time stated.

that the observed cells represented the remnant of a motion deprived of its driving force; circulation in a vortex may be shown to damp exponentially by viscous effects upon removal of the driving force (see Appendix, p. 66). For the circulation to have been wind-driven, therefore, a lull in the wind would have had to precede the moving ship by a short and constant distance. This event was improbable; flat surface conditions did not support such a contention. Also, the observed row spacing (1.5 m) was an order of magnitude less than the shortest spacing (20 m) reported by Faller and Woodcock (1964) for Langmuir circulations. These authors further observed that rows do not form with winds of Beaufort 2 or less (p. 27). Apparently, therefore, a driving force other than wind stress was acting on the system at the time of observation.

An alternative mechanism is the so-called thermohaline effect. By its effect on local density, transfer of heat and of water across the sea surface apparently was sufficient to produce the observed vortex system, or at least to sustain it after relaxation of wind stress. Formation of denser surface water is possible in spite of the heating effect of insolation. This is because short-wave solar radiation is absorbed throughout a few meters of water whereas the direct effects of long-wave back radiation and evaporation are confined to a surface layer about 1 mm thick. The form of cells in free convection, described by Bénard (1900), is generally hexagonal, with the sources (divergences) at the cell centers and the sinks (convergences) along the six-sided edges. To produce the elongated form of the cells observed, shear in the direction of the long axes is required. Since negligible shear at the air-sea interface was to be expected, the energy required to produce the observed strip-cell configuration must have been supplied at the lower boundary of the circulation. This is possible if, for example, the surface layer previously had been set in motion by wind stress. The expected tendency for cell axes to veer with inertial period (0.5 pendulum day) was not noted, possibly because the rows were observed for less than 1.5 hours under windless conditions. The direction of the wind that arose by 1400 PST (Fig. 2) prescribed thereafter the orientation of the rows. The extent to which the system of vortices was influenced by shear cannot be specified, and since the depth of the transient thermal structure could be established only once, no statement may be made as to whether the two sets of forces were in equilibrium.

Characteristics of the Vortices. The swimming velocity of oikopleurans found in the vortex system has been estimated to be -0.2 cm $\sec^{-1}$. An additional remark, that none of these highly visible animals was seen between convergence lines, permits the inference that the sampled population consisted only of oikopleurans that were successfully resisting downward transport by the water. Since some oikopleurans were seen at 5 cm below the sea surface, vertical velocity of water, w, at this depth did not exceed 0.2 cm $\sec^{-1}$. Further, if the distance within which w approached its single maximum value in the convergence plane was 5 cm or less, then $w_{\max} \approx 0.2$ cm $\sec^{-1}$ in this plane.

It is likely that the depth of the transient thermocline marked the lower limit of convective circulation on June 15 and 16. Therefore, if shear was applied at the lower boundary of the convecting cells, then this thermocline was the shear zone. Its noctural disappearance apparently was due to heat loss through the sea surface from the whole of the convecting layer. Diminution of the thermal magnitude, $\Delta_z\vartheta$, of the transient structure was obvious on the 17th and may be attributed to a surface-heating rate that barely exceeded the rate of downward transfer by wind mixing.

Components of the heat-budget equation may be grouped according to whether their instantaneous effect is confined to the upper centimeter or so of the water column. Under this convention, equation (1) becomes

$$Q_\Sigma = Q_r + Q_s,$$

where $Q_s = Q_b + Q_e + Q_c$, all essentially surface phenomena. In the absence of short-wave radiative transfer, i.e., during hours of darkness, $Q_r \approx 0$ and $Q_\Sigma = Q_s$.

On June 16, 1964, between 1930 and 2320 (PST), the average rate of net heat transfer in this area was

$$\bar{Q}_{\Sigma} = \bar{Q}_s = -0.105 \text{ cal cm}^{-2}\text{min}^{-1}.$$

Over the same period, the temperature of water overlying the shallow transient thermocline decreased by 0.4°C.[2]

Under the assumptions that temperature change in the convecting layer resulted from heat flux across only the air-sea boundary and that the convecting layer was isothermal from the sea surface to some depth, z_* (thermocline depth), this depth to which the change in thermal magnitude, $\Delta_t(\Delta_z\vartheta)$, took place had to be

$$z_* = -\frac{tQ_{\Sigma}}{c_p\varrho\Delta_t(\Delta_z\vartheta)} = 61.6 \text{ cm}, \qquad (Q_r = 0)$$

where $c_p = 0.956$ cal gm^{-1} °C^{-1}, $\varrho = 1.0246$ gm cm^{-3} and $t = 230$ min. Bathythermograms substantiate that this layer of water was isothermal. The depth z_* represents the lower limit of the vortical convective circulation during this period. The value of z_* calculated above is close to the depth derived from the theoretical ratio of cell width to depth reported by Stommel (1947: table II) for strip cells having one free and one rigid boundary. For the observed cell width $l = 150$ cm, cell depth, z_*, is predicted from Stommel's ratio to be 64.1 cm. These cell dimensions thus appear to be specified adequately by the theoretical method. Alternatively, the close agreement probably means that these semiempirical heat-budget calculations adequately describe net heat exchange at the sea surface.

The meteorological conditions recorded where the cells were observed are not unusual for this area in summer. Therefore, not considering the small heat loss from evaporation, heat fluxes similar to that on June 16 (Table II) are not unusual. It is, therefore, possible that vortex systems of the type observed occur widely and with sufficient frequency that their biological and physical consequences should not be ignored when considering near-surface oceanographic problems on small time scales. Masking and modification of the circulation by wind effects and absence of visible particles that can mark convergence lines may account for previous lack of comment on the widespread nature of the phenomenon.

Summary. Concentrations of the zooplankter, *Oikopleura longicauda* (Vogt), were observed along lines of convergent surface-water flow. Positive phototaxis observed in these animals aboard ship confirmed the possibility suggested by Bainbridge (1957) that this combination of physical and behavioral processes results in plankton concentration in parallel rows.

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[2] Measured by $\Delta_z\vartheta_{1930} - \Delta_z\vartheta_{2320} = \Delta_t(\Delta_z\vartheta) = 0.4$°C.

Estimated swimming speed of the animals was equated with downward water velocity in a vortex pattern. This velocity was 0.2 cm sec^{-1}.

Absence of wind suggests that the Langmuir circulation is unlikely; the thermohaline driving force is indicated as an alternate mechanism to produce the circulation.

Depth of the vortices was computed by equating observed temperature changes in the convecting layer with heat exchange across the sea surface. The result (61 cm) is close to the depth predicted from theory (64 cm).

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APPENDIX

Viscous damping of motion in a vortex can be shown by a development from the Navier-Stokes equation. Assumptions of incompressibility and constant viscosity of the fluid permit this equation to be written

$$\frac{\partial \vec{v}}{\partial t} - \vec{v} \times \vec{\zeta} = -\nabla\left(\frac{p}{\varrho} + \frac{v^2}{2} - \Omega\right) + \nu\nabla^2\vec{v} .$$

Taking the curl,

$$\frac{D\vec{\zeta}}{Dt} = (\vec{\zeta}\nabla)\vec{v} + \nu\nabla \times (\nabla^2\vec{v}) .$$

Noting that $\nabla\vec{\zeta} = 0$ and hence that $\nabla \times (\nabla^2\vec{v}) = \nabla^2\vec{\zeta}$, this becomes

$$\frac{D\vec{\zeta}}{Dt} = (\vec{\zeta}\nabla)\vec{v} + \nu\nabla^2\vec{\zeta} . \qquad (1)$$

Under the approximations that the motion is circular about the vortex axis, and that velocity is a function of distance, r, from the axis, we obtain from (1)

$$\frac{\partial\zeta}{\partial t} = \nu\left(\frac{\partial^2\zeta}{\partial r^2} + \frac{1}{r}\frac{\partial\zeta}{\partial r}\right),$$

which is satisfied by the solution

$$\zeta = \frac{vr}{4\nu t}\exp\left(-\frac{r^2}{4\nu t}\right).$$

Circulation after time t is then

$$C_t = \int_0^r \zeta\, 2\pi r dr = \pi r v_0\left[1 - \exp\left(-\frac{r^2}{4\nu t}\right)\right].$$

This equation exposes the exponential nature of damping of the circulation from its initial value, $C_o = \pi r v_0$. Rearranging terms to evaluate the time factor, we get

$$t = -\frac{r^2}{4\nu}\frac{1}{\ln[1 - (C_t/C_o)]} . \qquad (2)$$

A reasonable value for initial velocity in the convergence plane of a Langmuir circulation is 1 cm sec^{-1} (e.g., Langmuir 1938) so that, in a radius of 50 cm, $C_o = 157$ cm^2 sec^{-1}. After time t, this velocity is 0.2 cm sec^{-1} so that $C = 31.4$ cm^2 sec^{-1}. Taking 1 cm^2 sec^{-1} for the eddy value of kinematic viscosity, ν_e, we find that the time required for the circulation to damp to its observed state is 0.8 hour. Although other values of eddy viscosity are available for use in (2), it is seen that, in any case other than laminar, the circulation damps to some part (here, $20\,^0/_0$) of its initial value in a rather short time.

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Number of Circuli and Time of Annulus Formation on Scales of Pink Salmon (*Oncorhynchus gorbuscha*)[1]

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ABSTRACT

Mean numbers of circuli on scales of juvenile pink salmon collected along the coast of North America in 1964 increased from 1.7 on June 23 to 17.4 on September 10. On scales of adults collected from the eastern North Pacific Ocean from 1962 to 1965, mean numbers of circuli ranged from 24.1 on January 23 (1964) to 46.9 on September 2 (1962). The fork length at time of scale formation was approximately 60 mm. Mean fork length increased with the total number of circuli. The relationship of fork length to number of scale circuli showed some variation between stocks. The winter ring was present or was being formed on the majority of scales taken in late January. The development of the annulus varied considerably among individual fish.

INTRODUCTION

This paper presents data on the number of circuli and time of annulus formation on pink salmon scales taken from fish sampled along the coast of North America and from the eastern North Pacific Ocean. Samples of juvenile pink salmon were collected in 1964 from June 23 to September 10. Adult fish were collected from January 22 to September 2 on different dates in the years 1962–65. The samples were not examined by sex; it was assumed that the number of scale circuli does not differ with sex. This assumption was based on the findings of Enyutina (1963) with mature Asian pink salmon.

Circuli are ridges on the surface of fish scales. Under microscopic examination, pink salmon circuli appear as dark rings circling a point near the center of the scale. Circulus widths and distances between circuli vary. Groups of thin circuli lying close together are known as "checks" or "rings." The most common is a check found on scales after a year's growth — the annual ring or winter ring (Fig. 1). The annulus is the last narrow circulus of the winter ring.

The circuli and annulus are of interest in growth and racial studies of North American pink salmon. Little information, however, has been published on the circulus formation or on the time the annulus is laid down.

Pink salmon are taken in the North American commercial fisheries from Puget Sound, Washington, to Bristol Bay, Alaska. Adults enter the coastal streams in the fall and die soon after spawning. Their young migrate to sea the following April, May, and early June shortly after they emerge from the gravel bottom of the river. They spend the following year in the North Pacific

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Ocean or Bering Sea and then return to their natal stream to spawn at an age of 2 years.

EXPERIMENTAL PROCEDURES

SAMPLING

The study is based on seven samples of juvenile pink salmon containing 607 specimens, and 16 samples of adult pink salmon totaling 689 fish. Locations and dates of capture are shown in Fig. 2.

The juvenile fish were collected from June 23 to September 10, 1964. The samples of June 23, July 13, and August 1 were taken from a small boat with a hand-operated seine. A large purse seine with a small mesh bunt was used to capture the fish of August 14, August 31, and September 10. The sample of July 9 was taken with a trawl-type net towed near the surface by two vessels.

The adult fish were collected from January 22 to September 2, 1962–65. The samples of January 22, January 23, April 10, April 25, April 28, May 19, May 30, and June 25 were taken with Japanese longline salmon gear. A large purse seine was used to capture the fish of June 14, July 12, July 23, and July 26. The remaining samples were caught by Bureau of Commercial Fisheries research vessels by gill nets with mesh sizes of 2½, 3¼, 4½, and 5¼ inches, stretched measure.

SCALE SELECTION AND MEASUREMENT OF BODY LENGTH

Since variation of scale characters with respect to position on the body has been observed by Hayashi (1957), all scales were taken from a standard location on the side of the fish to minimize variability in circulus counts. For both juveniles and adults, the "preferred" scale was from a position two rows above the lateral line on the diagonal scale row which extends downward and posteriorly from the posterior insertion of the dorsal fin on either the left or right side of the fish. If both of these scales were missing or regenerated, the scale was taken slightly anterior or posterior to the "preferred-scale" position. This area included the first four scale rows above the lateral line and extended from a point directly below the posterior insertion of the dorsal fin to a point midway to the adipose fin.

Scales from adult fish were cleaned by rubbing between the fingers to remove the attached skin and were mounted with the sculptured side up on gummed paper. Plastic impressions of the mounted scales were made on clear cellulose acetate cards (Clutter and Whitesel, 1956). Scales from the juvenile specimens were scraped from the preferred body area with a scalpel and were mounted on glass microscope slides. The juvenile scale with the larger number of circuli was selected for use. A projection microscope was used to examine all scales at 100 × magnification (Mosher, 1950).

Measurements of fork length (distance from the fork of the tail to the tip of the snout) were taken from fish preserved in 10% formalin solution,

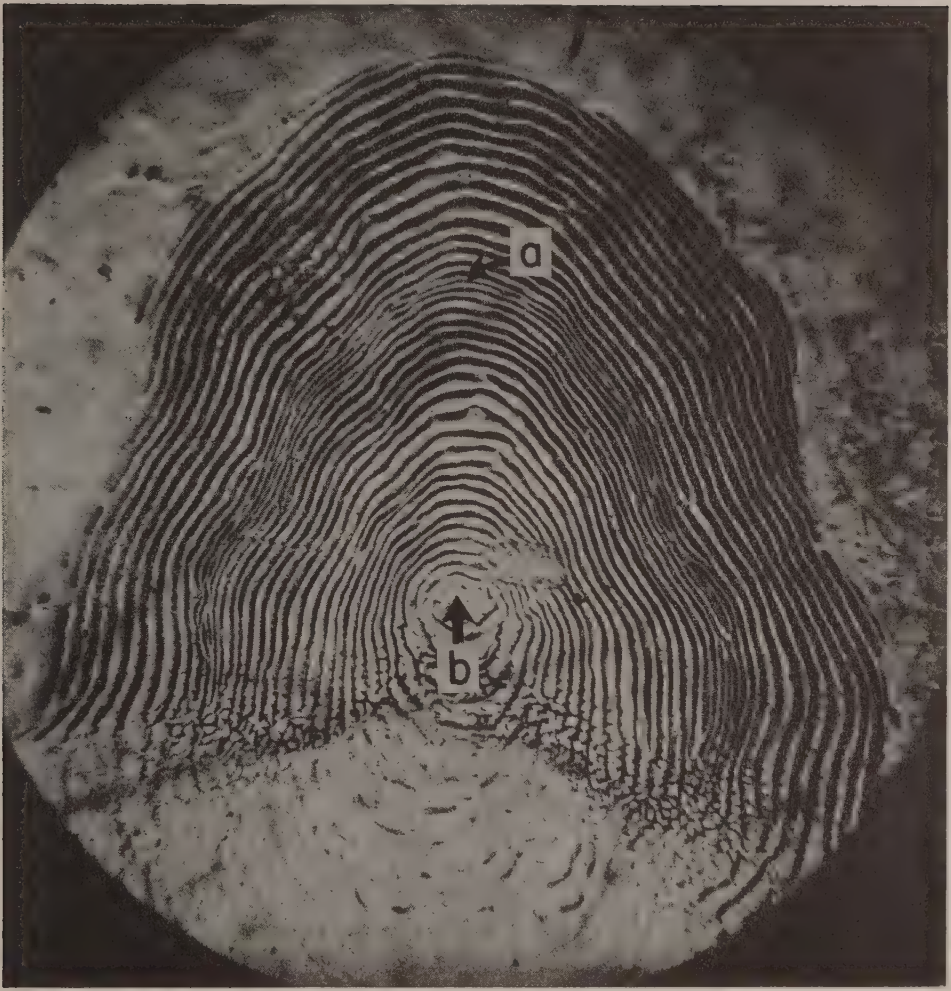

FIG. 1. Scale from an adult pink salmon showing the winter ring (a) and focus (b).

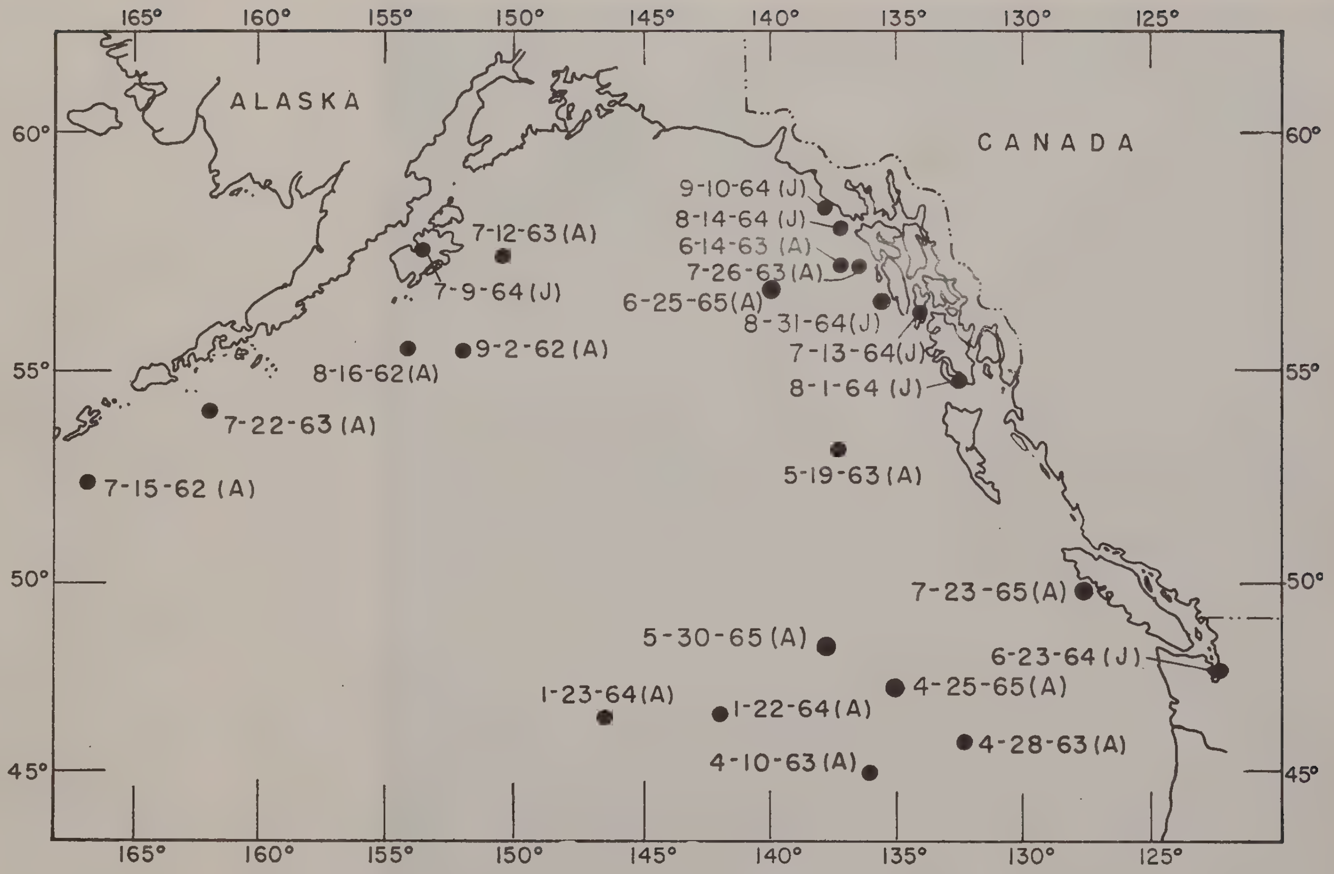
ALASKA
CANADA
165°
160°
155°
150°
145°
140°
135°
130°
125°
60°
55°
50°
45°
9-10-64 (J)
8-14-64 (J)
6-14-63 (A)
7-26-63 (A)
6-25-65 (A)
8-31-64 (J)
7-13-64 (J)
8-1-64 (J)
7-12-63 (A)
7-9-64 (J)
8-16-62 (A)
9-2-62 (A)
7-22-63 (A)
7-15-62 (A)
5-19-63 (A)
7-23-65 (A)
5-30-65 (A)
6-23-64 (J)
4-25-65 (A)
1-23-64 (A)
1-22-64 (A)
4-28-63 (A)
4-10-63 (A)

FIG. 2. Sampling locations and dates of capture of juvenile (J) and adult (A) pink salmon.

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from fresh dead specimens, and from anesthetized live fish. Length measurements taken from specimens preserved in formalin (samples of June 23, July 9, July 13, and August 1) were increased 5% to compensate for shrinkage (Shetter, 1936; Parker, 1963).

Selection of Scale Axis

The circuli on pink salmon scales form concentrically around a central platelet or focus (Fig. 1) on the imbedded portion of the scale. Although circulus counts can be taken along any axis from the focus, they vary with choice of radius (Pearson, 1964). To minimize variability among scales, all circuli were counted from specific radial lines. Two methods of selecting a scale axis were used in this study — one when scales had less than 16 circuli and another when scales had 16 or more circuli.

The method for scales with fewer than 16 circuli was as follows: (1) one end of a pair of dividers was placed in the center of the focus, (2) the most distant point on the periphery of the last circulus (the greatest distance from the center of the focus) was determined with the dividers, and (3) the line formed by the two points was the scale axis.

When scales have 16 or more circuli, the greater number of broken or branched circuli may make it more difficult to select the same axis repeatedly. Although the previously described method was faster, the following procedure gave more consistent results (Pearson, 1964): (1) the longest axis to the annulus was selected visually, (2) 17 circuli were counted out from the focus, along this axis, (3) one end of a pair of dividers was placed in the center of the focus, (4) the most distant point on the periphery of the seventeenth circulus was determined with the dividers, and (5) the line formed by the last two points was the scale axis. If the seventeenth circulus could not be used, the sixteenth was substituted.

RELATION OF CIRCULUS NUMBER TO DATE OF COLLECTION

Scales of juvenile pink salmon from Puget Sound were examined to determine when the first circulus was formed. Fish were captured April 14, April 20, April 29, May 4, May 11, May 19, and June 23. Only the fish in the sample of June 23 had scales. Two fish, 60 and 63 mm long, had scales without a circulus. Other specimens had scales with one, two, or three circuli. The number of circuli on scales at later dates could not be determined for this area because fish could not be located; scales of juveniles from Kodiak Island and the coast of southeastern Alaska were used instead.

The mean number of circuli on scales of juveniles became progressively larger with later sampling dates (Table I). The mean was 1.7 circuli on the Puget Sound scales of June 23 and 17.4 for fish taken off the coast of southeastern Alaska on September 10. The frequency distributions indicated that the range of circulus number was wide within certain samples (Table II).

TABLE I. Mean numbers of circuli on scales of pink salmon and mean fork lengths, by date of collection.

Locality	Life stage and date of collection	Number of fish	Mean number of circuli	Fork length (*mm*)	
				Mean	Range
		Juvenile			
Puget Sound, Washington	6-23-64	51	1.7	73.8	60–82
Uganik Bay, Kodiak Island	7-9-64	67	2.6	84.8	75–97
No Name Bay, southeastern Alaska	7-13-64	50	8.0	131.9	93–162
Kaigani Point, southeastern Alaska	8-1-64	115	10.7	154.8	135–193
58°12′N, 137°02′W	8-14-64	109	12.7	171.0	135–210
56°39′N, 135°30′W	8-31-64	111	15.3	193.3	135–235
58°32′N, 137°46′W	9-10-64	104	17.4	219.4	140–250
		Adult			
46°30′N, 142°09′W	1-22-64	15	25.4	308.0	245–365
46°30′N, 146°32′W	1-23-64	8	24.1	291.2	225–390
44°55′N, 136°08′W	4-10-63	23	29.7	376.5	335–455
47°05′N, 135°00′W	4-25-65	30	31.5	376.3	330–410
45°50′N, 132°15′W	4-28-63	41	31.3	389.6	345–505
53°17′N, 137°15′W	5-19-63	67	33.7	421.9	360–540
48°00′N, 137°40′W	5-30-65	33	36.3	465.0	390–550
57°23′N, 137°06′W	6-14-63	111	36.9	478.2	400–560
57°00′N, 140°00′W	6-25-65	90	36.8	473.3	415–545
57°37′N, 150°21′W	7-12-63	82	37.2	499.6	430–575
52°20′N, 166°58′W	7-15-62	66	36.4	486.2	429–536
54°01′N, 162°03′W	7-22-63	28	36.1	500.8	466–540
49°52′N, 127°36′W	7-23-65	15	46.3	545.0	460–640
57°18′N, 136°50′W	7-26-63	48	44.0	522.9	470–595
55°30′N, 154°03′W	8-16-62	17	40.5	522.1	477–600
55°32′N, 152°00′W	9-2-62	15	46.9	539.9	488–574

For example, the number of circuli on scales taken August 31 ranged from 9 to 20 and on September 10 from 9 to 22.

Generally, the total number of circuli on scales of adults increased through the collecting season (Table I). The mean number of circuli on scales taken in late January was approximately 25 and on September 2, 46.9. The mean values of the January 23, July 15, July 22, July 26, and August 16 samples were smaller than mean values from earlier samples. A possible reason for the small mean values on at least four of the five dates is discussed in the following section.

The range of circulus number was wide within all scale samples taken from adult fish (Table II). For example, the number of circuli on scales collected January 22 ranged from 18 to 33 and on June 14 from 30 to 46. The narrowest range, 43–50 circuli, was found in the sample taken September 2.

RELATION OF CIRCULUS NUMBER TO FORK LENGTH

The records of mean fork lengths and mean numbers of circuli (Table I) bring out the following two relationships: (1) the mean number of circuli

TABLE II. Numbers of fish listed in Table I with various numbers of circuli on the scales.

Date of collection	Number of circuli on scale																						
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
												Juvenile											
6-23-64	2	18	25	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
7-9-64	–	8	25	23	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
7-13-64	–	–	–	–	1	–	4	12	16	13	2	2	–	–	–	–	–	–	–	–	–	–	–
8-1-64	–	–	–	–	–	–	–	–	2	19	29	39	21	2	1	–	2	–	–	–	–	–	–
8-14-64	–	–	–	–	–	–	–	–	3	9	15	16	13	9	10	18	8	5	1	2	–	–	–
8-31-64	–	–	–	–	–	–	–	–	–	5	4	1	3	5	8	26	25	20	7	6	1	–	–
9-10-64	–	–	–	–	–	–	–	–	–	1	1	1	–	3	4	8	8	24	23	16	6	8	1

	Number of circuli on scale																																		
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
																		Adult																	
1-22-64	1	–	–	–	1	2	2	3	2	1	1	–	–	–	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1-23-64	–	1	1	–	2	–	1	–	–	1	1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4-10-63	–	–	–	–	–	–	–	–	1	3	4	5	2	2	2	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4-25-65	–	–	–	–	–	–	–	–	–	–	2	5	3	9	3	1	1	3	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4-28-63	–	–	–	–	–	–	–	–	2	3	2	6	4	8	2	3	3	3	2	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
5-19-63	–	–	–	–	–	–	–	–	–	1	1	1	4	8	10	7	8	10	6	6	3	1	–	1	–	–	–	–	–	–	–	–	–	–	–
5-30-65	–	–	–	–	–	–	–	–	–	–	–	1	1	1	1	3	3	2	7	3	2	2	3	2	–	2	–	–	–	–	–	–	–	–	–
6-14-63	–	–	–	–	–	–	–	–	–	–	–	–	1	–	3	11	10	7	20	14	18	11	5	3	3	1	1	2	1	–	–	–	–	–	–
6-25-65	–	–	–	–	–	–	–	–	–	–	–	–	1	3	2	5	7	13	12	13	12	5	6	4	6	–	1	–	–	–	–	–	–	–	–
7-12-63	–	–	–	–	–	–	–	–	–	–	–	–	1	1	2	5	9	9	7	10	8	10	7	7	5	–	1	–	–	–	–	–	–	–	–
7-15-62	–	–	–	–	–	–	–	–	–	–	–	–	2	–	1	5	8	10	10	13	3	5	4	1	3	–	–	1	–	–	–	–	–	–	–
7-22-63	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	3	1	5	4	3	5	4	1	–	–	–	–	–	–	–	–	–	–	–	–
7-23-65	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	1	3	4	2	3	–	–	–	1
7-26-63	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	3	2	6	3	5	8	6	6	2	1	2	3	–	–
8-16-62	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	2	1	1	3	3	2	–	1	1	–	–	–	–	–	–
9-2-62	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	4	–	3	1	3	2	–	–

and mean fork length both tended to increase as time progressed and (2) the mean number of circuli generally increased with an increase in mean fork length. Although the ranges in fork lengths for fish with the same number of circuli were wide, mean fork length clearly increased with number of circuli (Table III, Fig. 3). The rate of laying down circuli in relation to increases in length seemed to change at 23 and 33 circuli (Fig. 3). The change at 23 circuli occurred sometime in January or earlier, at about the time of formation of the winter ring. Fewer circuli were laid down per unit change in length between the 23 and 33 circuli than before or after.

TABLE III. Mean fork lengths of pink salmon, in relation to number of circuli on their scales.

Number of fish	Number of circuli	Fork length (*mm*) Mean	Fork length (*mm*) Range	Number of fish	Number of circuli	Fork length (*mm*) Mean	Fork length (*mm*) Range
2	0	61.5	60–63	5	26	344.0	320–370
26	1	73.8	65–83	9	27	344.4	285–385
50	2	78.7	70–87	11	28	362.3	335–395
29	3	85.1	76–94	18	29	370.3	335–420
12	4	91.3	86–97	19	30	396.4	350–462
–	5	–	–	34	31	403.1	355–500
4	6	116.0	109–119	28	32	421.9	360–515
12	7	125.2	113–147	47	33	450.9	355–538
21	8	136.2	126–150	51	34	459.2	380–530
47	9	142.9	128–160	63	35	461.9	350–526
51	10	153.2	140–168	72	36	468.8	330–530
59	11	156.2	140–172	66	37	479.7	395–540
37	12	162.9	153–185	54	38	487.8	420–540
19	13	176.7	150–205	42	39	495.6	415–600
23	14	186.3	161–210	29	40	495.0	415–575
52	15	192.4	150–220	27	41	509.2	440–545
43	16	200.6	167–230	24	42	510.0	460–560
49	17	211.7	185–245	11	43	511.3	450–553
32	18	222.5	195–245	13	44	526.5	495–580
25	19	222.6	190–245	17	45	539.8	500–595
8	20	236.9	225–250	12	46	531.1	495–640
8	21	237.5	230–250	7	47	530.9	488–585
4	22	252.5	210–300	5	48	530.2	460–595
2	23	282.5	255–310	5	49	538.4	513–569
3	24	291.7	285–300	5	50	550.6	506–580
3	25	315.0	310–320				

Shorter body lengths may account for the small mean numbers of circuli on scales of adults taken January 23, July 15, July 26, and August 16 (Table I). Fish taken on earlier dates were longer and had larger mean numbers of circuli. Enyutina (1963) also found greater numbers of circuli on longer pink salmon. Fish collected in the Amur River estuary that averaged 367 mm long had 24.9 circuli and fish that averaged 563 mm had 33.3 circuli.

The relation between fork length and number of circuli evidently differed between some stocks. Late in the 1963 season, fish taken off southeastern

Alaska that were approximately 50 cm long had a larger mean number of circuli than fish of comparable length taken east of Kodiak Island and south of the Alaska Peninsula (Table IV). A small number of circuli in relation to fork length was also observed in the sample taken south of Kodiak Island on August 16, 1962 (Table I).

Some information has been published on the body lengths of pink salmon and the number of circuli on their scales. Information available to the author is listed in Table V by dates and areas of collection. Most of the data were compiled from Asian fish. The results of these studies cannot be compared critically in all details for the following reasons: (1) different stocks were examined, (2) scales were taken from different areas of the fish, (3) circuli were counted on different radial lines of the scale, and (4) measurements other than fork lengths may be listed. The mean numbers of circuli and mean fork lengths of Table I and those of Table V merit two comments. First, scale samples from adult pink salmon from the eastern North Pacific Ocean appear to have larger mean numbers of circuli than fish of comparable size from the Asian spawning regions of Sakhalin, Kamchatka, and the Amur River. A similar difference was noted by Semko (1939) on the basis of his samples and the two scales collected by Gilbert (1913) in Bellingham, Washington. Second, the body length at the time of scale formation (approx 60 mm) was greater than that observed by Foskett (1951) and Vedenskii (1954). For example, mean fork lengths of fish with two scale circuli were 75.6 mm in Puget Sound and 81.8 in Uganik Bay. The mean body length of pink salmon from Iturup Island with two scale circuli was 44.8 mm in Vedenskii's study, and Foskett showed Vancouver Island pink salmon 52 and 57 mm long with four circuli. The results published by Foskett and Vedenskii were also somewhat different from the findings of Foerster and Pritchard (1943), who noted that scales were formed along the lateral line at 2¼ inches (60 mm). Although Neave (1943) did not present data, he also mentioned the "... comparatively large size attained by this species (pink salmon) before scale formation begins."

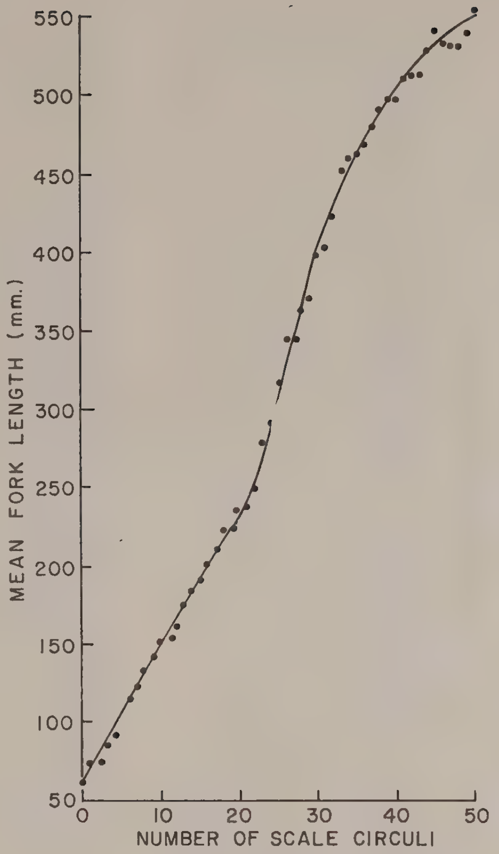
TABLE IV. Mean numbers of circuli on scales of pink salmon of the same range of fork length (48.5–51.5 cm) from widely separated Gulf of Alaska areas.

Area	Date	Number of fish	Number of circuli		Mean fork length (*cm*)
			Mean	Range	
Off southeastern Alaska	7-26-63	19	43.0	39–46	50.5
East of Kodiak Island	7-12-63	40	36.3	32–41	49.9
South of the Alaska Peninsula	7-22-63	14	36.1	31–39	50.2

TABLE V. Relation of body length to number of circuli on scales of juvenile and adult pink salmon in Asia and North America.

Dates of collection	Area	Number of fish	Average number of circuli[a]	Average body length[a] (*mm*)	Source
Juvenile					
July 7, August 4, 1946	Iturup Is. (USSR)	212	3 (1–7)	49 (30–80)	Vedenskii, 1954
July 13, 1950	Vancouver Island, B.C.	5	7 (4–10)	76 (52–105)	Foskett, 1951
September 19, 1959	East coast of Kamchatka	2	15	210	Birman, 1960
October–November	West coast of Sakhalin	–	17	230	Dvinin, 1952
Early November 1931	46°31′N, 138°19′E	5	14 (13–16)	– (200–225)[b]	Dubrovskaya, 1934
November 26, 1933	41°28′N, 131°00′E	2	16.5 (16–17)	225.5 (223–228)	do
Adult					
April 1959	Central North Pacific Ocean	47	28	410 (350–460)	Birman, 1960
Late June–July	Western Bering Sea	–	31	480	do
June–July 1948	West coast of Sakhalin	98	32.9	466	Dvinin, 1952
July 1948	East coast of Sakhalin	93	33.4	480	do
July 1929	Amur River (USSR)	10	32.9	546	Semko, 1939
July 1932	East coast of Kamchatka	42	32.9	532	do
July 1934	West coast of Kamchatka	100	28.1	423	do
July 1935	West coast of Kamchatka	98	31.1	472	do
July 1936	West coast of Kamchatka	100	31.6	496	do
August 2, 1910	Bellingham, Washington	1	51	635	Gilbert, 1913
August 3, 1910	Bellingham, Washington	1	50	559	do

[a] Range given in parentheses, where data are available.
[b] Salted specimens.



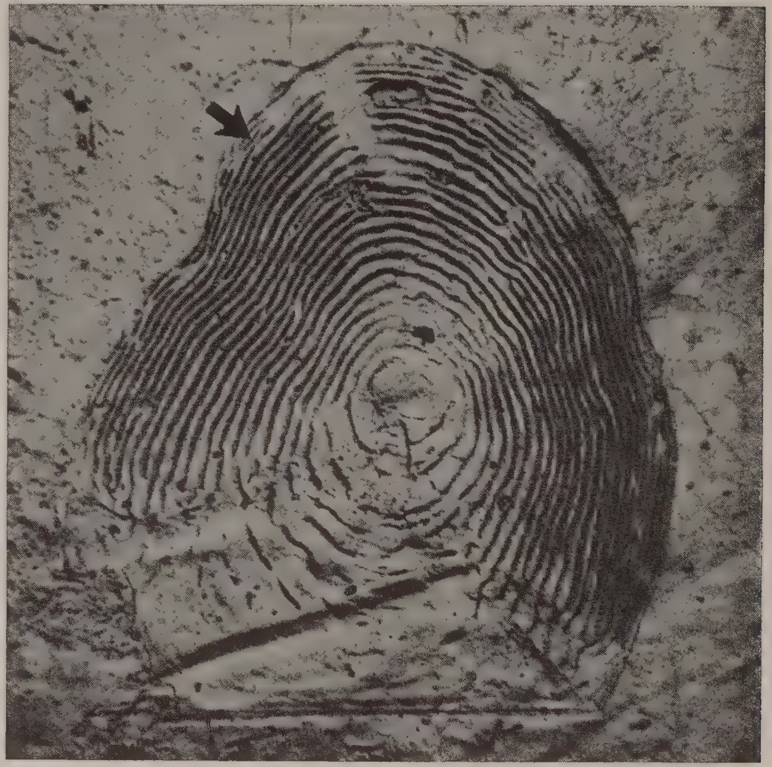


FIG. 3. (*Left*) Mean fork lengths of pink salmon, in relation to number of scale circuli (Table III).
FIG. 4. (*Right*) Scale collected January 23 showing the start of winter ring formation.

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TIME OF ANNULUS FORMATION

The winter ring is usually regarded as a winter "mark," formed when pink salmon are growing at a reduced rate. As few pink salmon have been captured on the high seas in winter, little factual information has been published on the time the annulus is formed within the ring. Vedenskii (1954) examined scales of pink salmon from the Kurile Islands and theorized that winter rings were formed in the spring. Birman (1960) examined scales collected in April from four east Kamchatkan fish. He found a winter ring and 7–13 additional circuli. Supported by this scale information and body length data, he stated that the ring was formed " . . . not later than the first half of January." Ricker (1964) used January 15 as the date of annulus formation. This was based on Birman's evidence and scales taken from three fish collected in the Gulf of Alaska, January 24 to February 1, " . . . which had 0, 2, and 2 circuli of new growth."

Scales from both juveniles and adults (Table I) were examined throughout the sampling sequence to detect the presence of annuli and determine dates of their formation. The first winter rings and annuli were found on the scales collected January 22 and January 23; rings were present or being formed (Fig. 4) on 22 of the 23 fish. The appearance of the scales varied considerably. For example, one scale exhibited no evidence of a winter ring while another scale had six circuli beyond the annulus. This variation indicated that the annuli were not being formed at the same time on the scales of all pink salmon. The next sample was taken April 10. All scales of adult fish collected on April 10 and later dates had an annulus.

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Body proportions and maturity of female lobsters. (By title only)

Six hundred female lobsters from the North Atlantic continental slope were measured to determine whether changes in body proportions could be used to indicate maturity. The width of the second abdominal segment was compared with the length of the carapace. The carapaces ranged from 48-197 mm; the shortest carapace of an egg-bearing female was 88 mm. The width of the abdominal segments ranged from 27-139 mm; in the smallest egg-bearing female it was 58 mm. All lobsters with a carapace length less than 88 mm had abdominal widths less than 58 mm and only 2.1% of the lobsters with a carapace measure longer than 88 mm had abdominal widths less than 59 mm. When plotted on probability paper, the measurements of the abdominal segments formed a sigmoid curve, indicating a bimodal distribution. The inflection of this curve was between 55 mm and 60 mm, closely corresponding to the size of this segment in the smallest egg-bearing female. Thus, the inflection represents the increased width of the abdominal segment as females approach and attain maturity. A similar analysis of inshore lobsters showed that the abdominal width was usually less than that of offshore individuals for a given carapace length, and that maturity occurred at somewhat larger carapace sizes in the coastal population. This difference, along with other morphometric craracters, may serve as a means of differentiating the two stocks.

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VERLAG PAUL PAREY · HAMBURG 1 · SPITALERSTRASSE 12

Multiple births in the northern fur seal

By Richard S. Peterson and William G. Reeder

Eingang des Ms. 23. 11. 1964

This paper describes three twin births in the northern fur seal *(Callorhinus ursinus,)* and subsequent behavior of mothers and young. To our knowledge, these are the first descriptions of multiple births among the Pinnipedia. They illustrate several adaptations to amphibious existence.

Northern fur seals live at sea, rarely touching land until summer, when they assemble on islands for parturition, copulation, and nurture of young to weaning age. The reproductive cycle includes a single post-partum estrus and delayed implantation, permitting a gestation period of almost exactly one year. Females leave their young within a few days after birth, returning in ten days (mean interval length) to nurse their pups for two days; this cycle is repeated continuously for four months following parturition. Individual recognition ability and highly concentrated milk permit females to feed at sea extended intervals, yet successfully rear their offspring on shore.

Fur seals, as well as other pinnipeds, generally give birth to single young each year. Bertram (1940) has suggested that uniparity in seals is advantageous, since parental care is highly demanding and mother-young mutual behavior is very specific. To the present time, however, statistics concerning the incidence of twinning in pinnipeds, or success of parturition and rearing of twins, have very seldom been reported. Twin fetuses have been mentioned as "rare" (see Harrison et al. 1952, p. 442, and Slipjer 1956, p. 42). In several genera, two young have been seen suckling one female; more accurate information has been lacking.

Methods

Approximately 50 male and 800 female fur seals were observed from a blind during three summers at Kitovi Rookery, St. Paul Island, Alaska, for study of social and reproductive behavior (r. s. p.). In 1961, the initial year, most of the animals were marked with large, individual, semi-permanent symbols bleached in the pelage. One of the 640 marked females gave birth to twins (Case I) as did an unmarked female at the same rookery (Case II). For close observation and recording of female-young vocalization at birth (w. g. r.), three pregnant females were captured and penned during July, 1962. One of these delivered twins (Case III).

A roentgenogram of the uterus of the post-partum female in Case III was made after the animal was tranquilized with propiopromazine (2.0 mg/kg), and strapped to a table. A cannula was passed through a medical sigmoidoscope in the vagina, and dilute aqueous iodide (manufactured for contrast radiography) deposited beyond the undilated cervix just prior to x-ray exposures. The female was released later, apparently unharmed.

Frequency of multiple fetuses

Northern fur seal twins were mentioned by VENIAMINOF (1839), though the first conclusive record was only recently published (NIGGOL and FISCUS 1960). During five years of pelagic research by the United States Fish and Wildlife Service, 4223 pregnant females were collected in the eastern Pacific Ocean and Bering Sea. Six of these females carried twins (FISCUS et al. 1964, p. 34). From the observed incidence (0.14 per cent), duplex implantation appears rare; successfull delivery of two living young may be even rarer.

Observations

Case I: On 25 June 1962, a marked female ("red x") delivered a single pup on Kitovi Rookery at 6:30 AM. She was known to have failed to raise a pup in 1961. The newborn, designated I-A, behaved normally, beginning mutual vocalization with its mother soon after delivery. The first irregularity in the process was noted ten minutes after the placenta had been delivered, when the female assumed a birth posture and again appeared to be in labor. The first pup was soon neglected, as its mother moved in a roughly circular pattern, dragging her hind quarters. At 7:00 AM, a second pup was born.

Vocalization between the mother and second pup (I-B) began, but at this point the first pup returned, evidently attracted by the sound. Pup I-A, 30 minutes older and slightly larger than its sib, was able to vocalize more vigorously. When the mother moved slightly in responding to I-A, the smaller I-B fell down an incline, dragging its placenta. The mother did not respond further to its feeble calling, nor did she attempt to retrieve it. Thus, the second pup was separated from its mother soon after birth, anchored a short distance away by its placenta, which had become caught in a crevice.

The pups (two males) were tagged 24 hours after birth, and I-B was freed when its placenta was taken for examination. This pup began wandering among females and was rejected by each one it approached, including its mother (Figure 1). Little or no preference for its own mother was evident in the behavior of this pup. It wandered for two weeks, becoming very emaciated. Apparently it had never nursed when it finally disappeared from the rookery on the 16th day after birth.

The mother continued to suckle I-A in the usual manner. She came into estrus on 30 June, copulation ensued, and she departed for sea the following day. She returned on 7 July, searched for and located I-A, and nursed for two days. Similar cycles followed until 31 October 1962, when the pup apparently was weaned. In 1963, this female was not observed.

Case II: Another twin birth was observed on the same rookery, but the female had not been marked and could not be identified with certainty for long after the delivery. The twon pups were born on 10 July 1962, at 3:30 and 3:40 PM; the mother was never observed nursing both. It appeared that one of the pups was rejected shortly after birth.

Case III: On 15 July 1962, a pregnant female was captured on Northeast Point Rookery, and temporarily confined in a slat cage. On the following day about 4:30 PM, the first pup (III-A) was born. Delivery appeared normal. Mutual vocalization began within the first minute and continued for a little over 20 minutes,

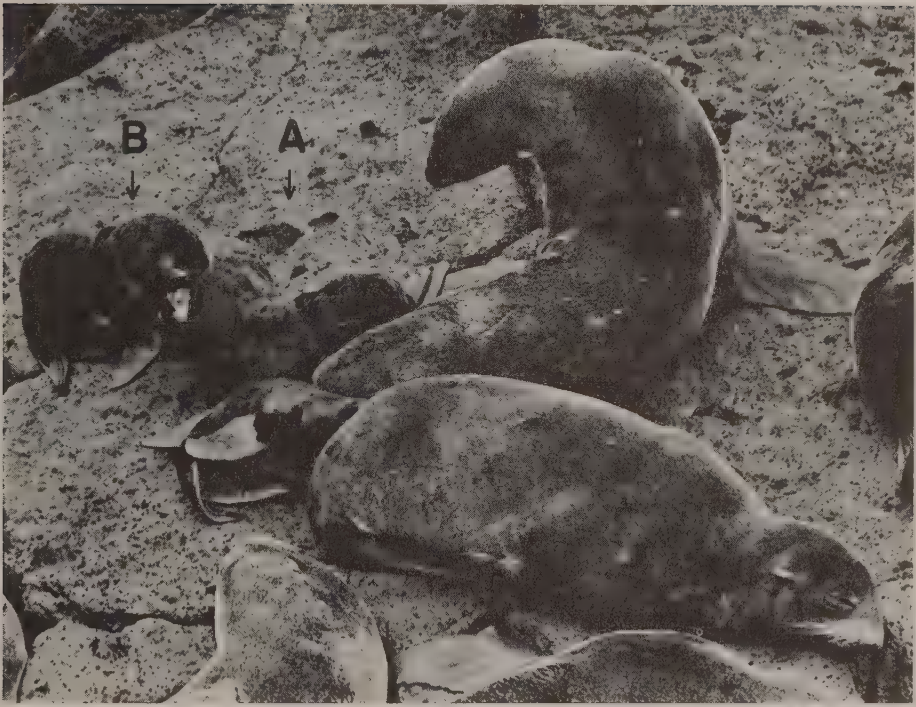

Fig. 1. Female fur seal and twin pups described as Case I. The pup (I—A) nursing in this photograph was reared normally. The other (I—B), left, never developed mutual recognition with its mother and eventually died.

though the rate of calling by the mother declined strongly after the first 12 minutes, when she seemed to be experiencing pain. The placenta had not been delivered.

Approximately 25 minutes after the birth of the first pup, the second (III-B) appeared, followed shortly by a single placental mass. Pup III-B began calling shortly after birth, but elicited minimal response from its mother, which was very quiet and moved little for nearly an hour. Her occasional vocalization evoked responses from both pups. The pups vocalized almost continually, calling and responding to each other, in a pattern and frequency similar to that noted in mother-young mutual calling after a normal single birth. Since the mother failed to vocalize consistently in response to the pups, it seems unlikely that recognition of the female's individual call could have developed in either pup.

At one day of age, the two pups (females) were weighed (A = 5.8 kg; B = 5.3 kg). The mother was allowing both to suckle. III-A was clearly stronger and more active, and its knowledge of the mammary position soon became quite accurate. III-B, however, fed for fewer and shorter periods and never developed accuracy in its location of the nipples, often requiring appreciable periods of hunting prior to suckling.

Confinement of this female undoubtedly affected her behavior in accepting both pups. Eugene T. Lyons (personal communication) found that captive female fur seals could be induced to accept pups other than their own. This was never observed on Kitovi Rookery, where more than 200 mother-young pairs were marked and carefully observed.

The placenta, originally a single mass, broke apart shortly after the birth of III-B,

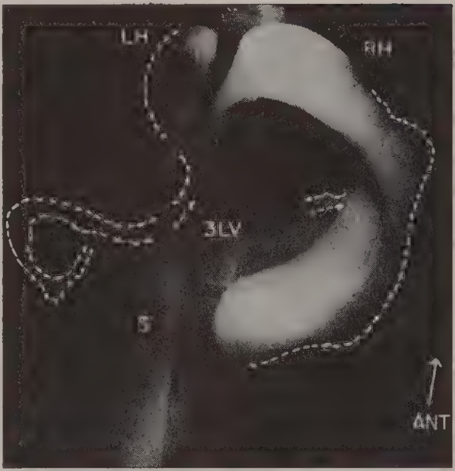

Fig. 2. Roentgenogram of iodide-filled uterus of female fur seal in Case III. Five days postpartum. Dorsal view. LH Left Horn of uterus, RH Right Horn of uterus, 3LV 3rd Lumbar Vertebra, S Sigmoidoscope with cannula protruding at top, ANT Anterior direction.

a section remaining tethered to each pup. This connection suggests unilateral implantation. Five days after parturition, a roentgenogram was made of the uterus (Figure 2), demonstrating enlargement of only the right uterine horn.

After the x-ray was taken, the mother and two pups were released on Kitovi Rookery and kept under observation. The mother came into estrus and accepted copulation; the pups remained near her through this period. Two days after release, the mother departed to sea and was not later observed, perhaps due to her release on a rookery otherwise strange to her. The two pups wandered separately and extensively, and one was observed twice near the former inland location of the cage in which it had been born, above the rookery. Five days after the departure of the mother, both pups (now aged ten days) left the rookery for the final time. One was not seen again; the second was found three days later about $^3/_4$ mile (1,2 km) inland on a truck road. It died shortly thereafter in captivity.

Discussion

There are physiological and social disadvantages to multiple young in pinnipeds. Among the Phocidae, prodigious growth of the newborn pup requires a very large quantity of milk, such that "one doubts [a female's] ability to provide in this way for two pups simultaneously" (Bertram 1940, p. 27). Young fur seals (Otariidae) grow more slowly, but must store enough nourishment at each nursing to survive and grow through regular fasts while their mothers are feeding at sea. Although marine mammals have the most concentrated milk of any yet tested, (see Kooyman 1963) we are not sure that any seal could supply sufficient milk to raise two pups to weaning.

The process of locating one particular pup among thousands on a fur seal rookery is complex, and sometimes a mother searches for several hours before finding her own. The problem would be compounded if multiple young were involved. Further, if two young should be accepted, as has been suggested in Case III, perhaps mutual calling sequences would not develop adequately with either pup. Young respond to vocalization of the mother at birth, but evidently must learn individual recognition postnatally, especially during the first day. This was emphasized by the lack of recognition between the mother and the second pup in Case I.

Annual alternation of the implantation site between the two uterine horns is usual in fur seals. Thus, an embryo begins development in a resting horn. Perhaps twins could not develop bilaterally in a female which had been pregnant the preceding year, for only one horn would be resting. In Case I, the only individual whose history is known, no pup was born the year preceding the birth of twins; implantation may have been bilateral since there were two placentae. Records for other twins show five unilateral, and three bilateral implantations (Fiscus et al., op. cit.).

The evidence that one pup is rejected by its mother if twins are born, and the extreme rarity of twin fetuses, support the idea that natural selection has favored uniparity in fur seals.

Acknowledgements

The help of the following is gratefully acknowledged: Dionisy Bourdukofsky, James Nybakken, David Dixon and Eugene Lyons; Abbott Laboratories, Wisconsin Alumni Research Foundation, Johns Hopkins University (in part through USPHS grants GS–146 and E–2415), and the Marine Mammal Resources Program, [United States] Bureau of Commercial Fisheries. One of us (R. S. P.) worked under the direction of William Sladen and Ford Wilke; their help is appreciated.

Summary

Three examples of twin births in the northern fur seal are described. In no case were two young raised to weaning age. The very low incidence of duplex implantation appears to be one of a remarkable series of adaptations permitting successful rearing of young.

Zusammenfassung

Es werden drei Berichte über Zwillingsgeburten bei der nördlichen Pelzrobbe gegeben. In keinem Fall wurden zwei Junge bis zur Entwöhnung aufgezogen. Das sehr seltene Vorkommen von doppelter Implantation scheint eine der bemerkenswerten Anpassungen für erfolgreiche Aufzucht eines Jungen zu sein.

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International co-operation in the Indian Ocean

Collective research in the Indian Ocean has been one of the more important recent achievements of oceanography. This work has yielded information about one of the most neglected ocean areas, and the results will be of great economic significance for the many populations living around this broad ocean. More than 20 nations took part in the research programme sponsored by UNESCO.

In December 1964, the U. S. research ship, *Anton Bruun* (Fig. 1), completed its last mission for the International Indian Ocean Expedition (IIOE) and sailed for the United States. In 2 years, the *Bruun* completed nine scientific cruises covering a distance of more than 116,000 kilometres in the Indian Ocean (Fig. 2). Today, 8 months after the end of the field programme, we are still asked such questions as: What is the International Indian Ocean Expedition about? What is the scope of the Expedition? What are some of the results of the Expedition?

With reference to the last question, it is too soon to describe and assess the scientific contributions of the Expedition accurately. The mass of accumulated data will take time to analyze, so the results will continue to be published for years to come. At present, we can only briefly review the background of the Expedition and present a few highlights of the *Anton Bruun* cruises.

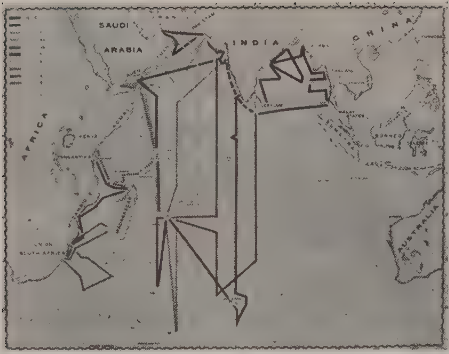
The idea of an international oceanographic programme was first proposed at a meeting of the Scientific Committee on Oceanic Research (SCOR) held in Paris in 1957. The plan developed at the meeting was to apply to a single ocean basin the kind of complex international scientific cooperation that produced such fruitful results during the International Geophysical Year (IGY). The Indian Ocean was selected for this extensive study because so little was known about this body of water, which covers one-seventh of the earth's surface. In addition, it was felt that the knowledge gained from the Expedition would lead to increased utilization of the natural resources of the Indian Ocean and adjacent seas by the more than 500 million people living around the border of these waters.

The Expedition began in 1961, reached a peak in 1963, and has since tapered off. No termination date has been set, since it was hoped that countries bordering the Indian Ocean will continue to pursue the types of research undertaken during the early years of the Expedition. To date, 25 countries utilizing more than 40 research ships have participated in the field programme.

1

As plans of participating countries developed, it became apparent that if the objectives of scientists were to be met, it would not be possible to lay down rigid cruise patterns for all of the ships. Consequently, each country agreed to devote approximately one-half of each cruise to collecting data for systematic surveys and the remainder to individual interests of its scientists.

Studies carried out during the Expedition covered the entire range of modern oceanography. Included were studies in meteorology, physical and chemical oceanography, submarine geology, and the various specialized fields in marine biology.



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The programme in biology, representing only one part of the total U. S. contribution to the International Indian Ocean Expedition, was supported by the National Science Foundation, with the major effort being based on a series of nine cruises of the *Anton Bruun.*

Descriptions of a few highlights of the cruises follow. To a considerable degree, the topics selected reflect the authors' own major interests. They do not necessarily represent the most important accomplishments of the cruises; such judgment must await completion of the vast number of studies now under way in the laboratory.

Productivity. – Reports by merchant ships and casual observations of opportunity by research vessels of mass fish mortalities and large plankton blooms in the Western Arabian Sea have long suggested that the production of life in these waters must be high. Accordingly, a cruise was made by the *Anton Bruun* in the Western Arabian Sea in October-November 1963 to investigate this area of indicated high productivity (Fig. 3). Extremely fertile waters were found in an area of diverging currents located some 240–320 kilometres off the Arabian Coast. In terms of carbon assimilation, primary productivity in these waters was an order of magnitude greater than that of the oceans as a whole. At two stations off the Gulf of Oman, rates of productivity were 5.7 and 6.4 g carbon/m^2/day–values considerably higher than ever before reported for the open sea. Dense phytoplankton populations of bluegreen algae, dinoflagellates, and diatoms were commonly observed at the surface between the Arabian Coast and the diverging-current region offshore. The plankton production was characterized by a patchy distribution. While on station, the *Anton Bruun* would commonly drift through areas of extremely dense plankton blooms, which varied in diameter from a hundred metres or less to several kilometres.

Results of this cruise offer an explanation of the probable course of events causing previously reported mass fish mortalities in the Western Arabian Sea. The concentration of dissolved oxygen was observed to decrease rapidly with depth, reaching less than 1.0 ml/litre at 100 metres and less than 0.1 ml/litre at mid-depths of 500 to 1000 metres at some stations. Sinking and decomposition of organic matter could create anaerobic conditions. Subsequent mixing of this anoxic water with surface water might easily lead to the death of fishes.

Mollusks. – Rich hauls of snails (Gastropoda), tooth shells (Scaphopoda), and bivalves (Pelecypoda) were dredged and trawled by the *Anton Bruun* from the ocean floor in the Gulf of Oman.

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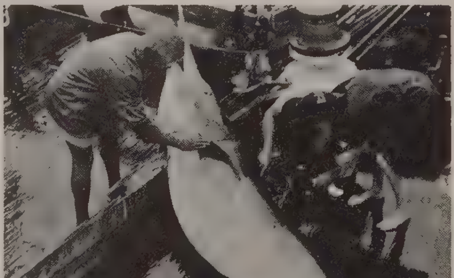

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One 5-minute trawl haul made at a depth of 82 metres yielded 90 kilos of shells. The most exciting mollusks caught were 5 adult and 12 juvenile snails, *Strombus listeri*. Prior to the *Bruun*'s find, only 5 specimens of this species had been reported. All the latter were found 70 years ago off Ceylon and Burma.

Bottomfish. – Trawling surveys to assess the latent bottomfish and shellfish resources of the Arabian Sea and Bay of Bengal were made on two cruises of the *Anton Bruun*. Both cruises yielded specimens and data of great scientific interest that will help to describe Indian Ocean fauna and contribute to an understanding of the relation of its benthic fauna to physical and chemical oceanographic features of the region.

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Largest trawl catches were obtained in the Western Arabian Sea in the same general area where, on the immediately preceding cruise, very fertile waters (as measured by primary productivity) had been observed. Considering the small size of the trawl nets used, two successful trawl hauls made off the Southeast Arabian Coast yielded exceedingly large catches of fish. One 30-minute haul produced 2 545 kilos; the other, of 45-minutes duration, yielded 773 kilos of fish and 836 kilos of swimming crabs (Fig. 3). Together, these two hauls produced almost as much fish as was caught in the remaining 84 trawl hauls made on the Arabian Sea cruise.

Most of the fish caught in trawls off Arabia were stingray, the largest specimen weighing 204 kilos. The second most abundant fish caught off Arabia was grunt, a desirable food fish.

Bathypelagic Fish. – Midwater trawl nets were used on several cruises to catch bathypelagic fishes over a wide range of depths. Two midwater trawl catches were of unique zoological interest. One haul contained a leptocephalus, or larval stage of a deep-sea eel, which was bright orange-red. All other known eel larvae, which number in the tens of thousands, are transparent. The other exciting specimen captured was a metamorphosing eel, over 1 metre long. Identification of this eel is presently in doubt. On the one hand, it seems referable to the "giant lepto-

7

cephalus" caught years ago by the Danish research ship *Dana*. On the other hand, it may be an adult nemichthyoid or snipe eel.

Pelagic Fishes. – Japanese-type longline gear was fished on two cruises of the *Anton Bruun* (Fig. 4). Inasmuch as a Japanese commercial longline fishery has operated in the Indian Ocean since the early 1950's, studies from the *Bruun* were designed to aid in understanding the interrelations between species and to delineate the distribution of these pelagic fishes in relation to their environment. Preliminary analyses of the data indicate an intimate association of certain species with specific types of water. For example, all of the albacore tuna caught on the two cruises were taken in the more southerly latitudes in waters identified as South Indian Ocean Central Water Type. Nearly 400 tunas were caught with the longline gear. Other pelagic fishes that were caught included the various species of billfishes (Fig. 5) wahoo, sharks, lancet fish, and the unusual moonfish (Fig. 6).

One of the most fruitful aspects of the programme was the opportunity for scientists to exercise a high degree of personal judgment in attaining their particular research goals. Of equal importance was the international aspect of shipboard activities (Fig. 7). Excluding the permanent staff assigned to the vessel, approximately one-fourth of the scientists participating on the cruises of the *Anton Bruun* were from countries other than the United States. Researchers from Australia, Austria, Brazil, Denmark, Egypt, Hong Kong, India, Israel, Italy, Madagascar, Pakistan, South Africa, Spain, Sweden, Thailand, and Zanzibar were included in the scientific complement.

The fondest memories of cruise participants are the friendships they formed with scientists of other countries. The general feeling of scientists concerning the programme aboard the *Anton Bruun* was expressed in a letter written by a participant from India, a portion of which is quoted below:

> "I very much appreciated the brotherly attitude of the scientific staff, all working in a team, imbibed with the spirit of exploration and pursuit of knowledge and, at the same time, with individual freedom and choice. I enjoyed this inspiring experience and also the hospitality, for which I am certainly grateful to the United States Programme in Biology of the International Indian Ocean Expedition."

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Figure 1
U.S. research vessel *Anton Bruun* at anchor off Phuket, Thailand.

Figure 2
Cruise tracks of the *Anton Bruun* during the International Indian Ocean Expedition, 1963–1964.

Figure 3
Trawl catch of swimming crabs and grunt fish taken off southeast Arabia.

Figure 4
Storing longline fishing gear on the stern of the *Anton Bruun.*

Figure 5
Examining a large white marlin for external parasites.

Figure 6
A large longline-caught moonfish (opah).

Figure 7
Shallow-water fishes collected at Astola Island, West Pakistan, are examined by Dr. H. G. Kewalramani, Indian Department of Fisheries.

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The Relation of Menhaden to Estuaries

John W. Reintjes and Anthony L. Pacheco

The Relation of Menhaden to Estuaries

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ABSTRACT

Menhaden, genus *Brevoortia*, use estuaries along the Atlantic and Gulf coasts of the United States as nursery areas for more than half of their first year of life. The Atlantic menhaden, *B. tyrannus*, and Gulf menhaden, *B. patronus*, support the largest fishery in North America and observations reported concern mainly these species. Spawning occurs in the Atlantic Ocean and Gulf of Mexico. After hatching and early development the larvae move into estuaries. The time spent in the ocean before entering the estuaries is not known. Larvae move into the tributaries near the upstream limits of saline water. Water temperatures below 3 C deter entry into the estuaries, inhibit movements into the tributaries, and cause mass mortalities. Temperatures below 3 C killed larvae confined in the laboratory at salinities of 24‰ but effects varied somewhat with acclimation temperatures. Larvae and juvenile menhaden were collected in salinities of 1‰ or less along the Atlantic and Gulf coasts of the United States. Along the south Texas coast juveniles survived salinities up to 60‰ but were killed by 80‰. Other physical, chemical, and biological factors affecting young menhaden are mentioned but supporting data are few. Literature citations include most of the publications on the estuarine phase of the menhaden's life history.

INTRODUCTION

Most common commercial and sport fishes of the Atlantic and Gulf States live in estuaries during part of their life cycle. None of these fishes are so widely distributed and abundant as the menhaden, genus *Brevoortia*. Menhaden support the largest commercial fishery in North America and also provide forage for many carnivores. Most, perhaps all estuaries from New England to the Mexican border are utilized by schools of juvenile menhaden. The association of menhaden with estuaries for the greater part of the first year of life appears to be a persistent, if not a necessary, aspect of the life history. References to the occurrence, distribution, and other aspects of the estuarine biology of menhaden not cited in this report are included in annotated bibliographies by Reintjes, Christmas, and Collins (1960) and Reintjes (1964a). Although this report principally concerns the Atlantic menhaden, and to a lesser extent the Gulf menhaden, a brief summary of the distribution of juveniles of additional species of menhaden is given to introduce the problems of menhaden and estuaries.

DISTRIBUTION

Young Atlantic menhaden, *B. tyrannus*, were recorded in Canada by Leim and Day (1959) but their occurrence in waters that far north was unusual. The customary range extends from the Gulf of Maine (Scattergood, 1948; Scattergood, Trefethen, and Coffin, 1951a, 1951b) to central Florida (Goode, 1879; June, 1958; Sutherland, 1963). Juvenile menhaden usually occupy the estuaries between these geographical limits from May to October. Juvenile yellowfin menhaden,[1] *B. smithi*, are limited in distribution from Sapelo Island, Georgia, to Tampa Bay, Florida (Suttkus, 1958; Springer and Woodburn, 1960; Reintjes, 1962, 1964b; Tabb and Manning, 1961, 1962). Young Gulf menhaden,[1] *B. patronus*, occurred in collections from southern Florida to the Mexican border; the principal region of abundance was from Apalachicola, Florida, to Galveston, Texas (Suttkus, 1956; Gunter, 1956; Reid, 1957; Arnold, Wheeler, and Baxter, 1960; Gunter and Christmas, 1960). Distribution of juvenile finescale menhaden, *B. gunteri*, seems to be only from Matagorda, Texas, to the Gulf of Campeche in the western Gulf of Mexico.

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[1] Common names of two species of menhaden do not agree with American Fisheries Society (1960). "Yellowfin shad" was proposed by Hildebrand (1919) in the original description of *Brevoortia smithi* from specimens collected at Beaufort, N. C., where "shad" is the vernacular name for menhaden. No distinguishing common name is in use among fishermen in Florida, the only area where it is caught commercially. Therefore, yellowfin menhaden is used for greater conformance to the accepted generic common name. "Largescale menhaden" was proposed as the common name for *Brevoortia patronus*, probably to shorten "largescale Gulf menhaden" used by Hildebrand (1948). The deletion was a poor choice, for "Gulf menhaden" has been used as the common name for nearly a century (Goode, 1879; Jordan and Evermann, 1896).

The areas of principal abundance are limited to Copano Bay, Corpus Christi Bay, and Laguna Madre of Texas and Laguna Madre of Tamaulipas (Gunter, 1945; Hildebrand, 1948, 1955, 1958, 1963; Breuer, 1957; Simmons, 1957; Christmas and Gunter, 1960; Gunter and Christmas, 1960).

SPAWNING AND EARLY DEVELOPMENT

Atlantic menhaden spawn in oceanic waters along the Continental Shelf (Reintjes, 1961), including Long Island Sound (Perlmutter, 1939; Wheatland, 1956; Richards, 1959), Narragansett Bay (Herman, 1963), and the Gulf of Maine (Bigelow and Schroeder, 1953; Marak and Colton, 1961; Marak, Colton, and Foster, 1962). Some spawning apparently occurs every month from May to October off New York and New England, in March and April and again in September and October off the Middle Atlantic States, and from November through March off the South Atlantic States (Higham and Nicholson, 1964). Heaviest spawning apparently is off North Carolina.

Although the depth at which menhaden spawn is not known, eggs and larvae were collected in oblique tows from 70 m to the surface during cruises of the *Theodore N. Gill* (Reintjes, 1961). Personnel of the Institute of Marine Science of Virginia collected eggs and larvae in surface plankton tows in the Atlantic Ocean off the Virginia Capes (Massmann, Norcross, and Joseph, 1961, 1962, and personal communications).

Hatching of eggs and early development of larvae also occur in the ocean. Embryos and yolk-sac larvae from eggs collected in nets near Woods Hole, Massachusetts, were described and sketched by Kuntz and Radcliffe (1917). They concluded that eggs hatched in 2 days at 15 C, and that the yolk was absorbed completely 5 days later. The smaller size of larvae in the ocean than in the estuaries gives further evidence of oceanic spawning (June and Chamberlin, 1959; Reintjes, 1961; Massmann, Norcross, and Joseph, 1961, 1962; Pearcy and Richards, 1962).

MORPHOLOGICAL CHANGES DURING METAMORPHOSIS

Larvae undergo morphological changes when they transform into juveniles. At the time of entry into the estuaries, larvae are slender, transparent, and nearly colorless except for several rows of melanophores. Their fins are partially formed, they have no scales, and their mouths and eyes are large. In contrast, juveniles have deep bodies, well developed fins, ventral scutes, scales, and a large head. Internal changes during metamorphosis mainly concern the method of feeding and the digestive tract: gill rakers elongate and branch to form a basket-like sieve; a complex structure develops in the pharynx, presumably to accumulate the collected plankton; a muscular pyloric stomach or gizzard develops; and the intestinal tract elongates and coils. These changes are normally associated with the change from a selective, particulate-feeding carnivore to a nonselective, filter-feeding omnivore. No description has been published of late larval development or metamorphosis of Atlantic menhaden. Suttkus (1956) described the development and transformation of Gulf menhaden with proportional measurements, photographs, and detailed accounts of fin formation, pigmentation, and other external characters. Generally, the species are similar except for size. Apparently, Gulf menhaden are smaller than Atlantic menhaden at all stages of development from embryo to adult.

TIME OF ENTRY INTO THE ESTUARINE NURSERY AREA, AND SIZE

Larvae enter estuaries from May to October in the New England States (Kuntz and Radcliffe, 1917; Perlmutter, 1939; Warfel and Merriman, 1944; Bigelow and Schroeder, 1953; Wheatland, 1956; Richards, 1959; Herman, 1963); the period is October to June in the Middle Atlantic States (Hildebrand and Schroeder, 1928; Pearson, 1941; Massmann, 1953, 1954; DeSylva, Kalber, and Shuster, 1962); and December to May in the South Atlantic States (Deubler, 1958; Tagatz and Dudley, 1961). Larvae were 14 to 34 mm, fork length, when they entered the estuaries. At Indian River Inlet, Delaware, 1958–61, the earliest time of entry was October 25 and the latest, June 11. The mean monthly catch per haul and range of fork lengths for these Indian River fish are given in Table 1.

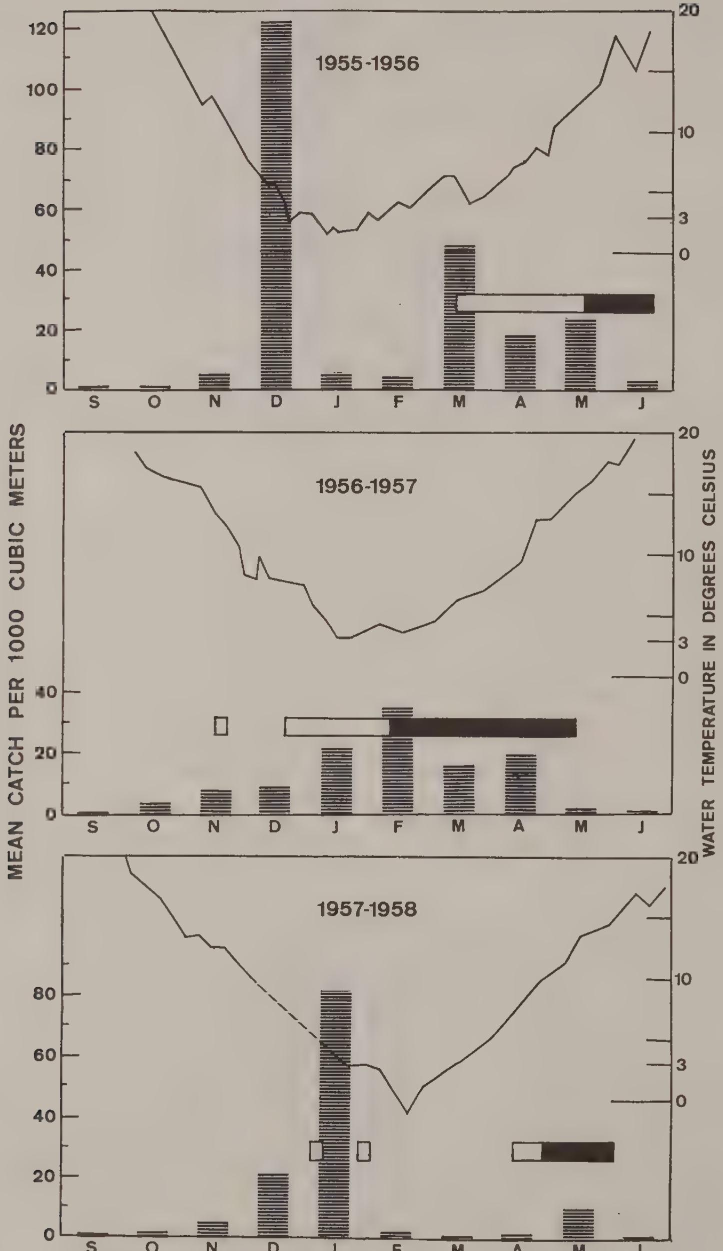

FIGURE 1.—Catches of menhaden larvae and water temperatures in the inlet compared to catches of larvae in a tributary, by month, Indian River, Delaware, 1955–58. The vertical bars represent monthly weighted geometric mean catches of larvae at the inlet during night flood tides. The horizontal bars represent weekly catches at the nursery area (open for 1 to 10 and solid for more than 10). The line graph shows the weekly mean water temperatures at the inlet during flood tides (from Pacheco MS).

EFFECTS OF TEMPERATURE AND SALINITY ON MENHADEN

The combined influence of weather, tides, and river flow can subject estuarine organisms to rapid changes in temperatures and salinities. The effects of temperature and salinity on marine and brackish water animals has been reviewed by Kinne (1963, 1964). He stated (1963, p. 301):

> "Temperature and salinity are two of the most potent physical factors in the life of marine and brackish water organisms. They largely characterize the physico-chemical properties of a given body of water. It has become increasingly evident from numerous papers that both factors should be considered together. There exists a complex correlation between the biological effects of temperature and salinity, the 'temperature-salinity relation' (tsr): temperature can modify the effects of salinity and change (enlarge, narrow, shift) the salinity range of an organism, and salinity can modify the effects of temperature accordingly. . . ."

Although menhaden occur in a wide range of temperatures (0 to 40 C) and salinities (0 to 60‰) the effects of these extremes on survival, metamorphosis, and growth are not well known, and even less is known of the combined effects of temperature and salinity.

Temperature

The collections at Indian River, Delaware, appeared to show a relation of temperature to time of entry into the estuary and, subsequently, to movements and survival within the estuary. The water temperatures, catches of larval menhaden at the inlet and catches at a nursery area nearly 12 miles above the inlet at the base of Millsboro Dam were compared from December to June, 1955–56 and from September to June, 1956–61[2] (Figs. 1 and 2). Comparison of the occurrences of the larvae at the inlet with their subsequent appearances or absences in the tributary nursery area indicate that a water temperature 3 C may be critical. This conclusion is in agreement with June and Chamberlin (1959).

TABLE 1.—*Mean monthly catch per plankton net tow of Atlantic menhaden larvae and range of fork lengths in mm (in parentheses) from Indian River, Delaware, 1958–61*

[From Pacheco]

Month	Year 1958–59	 1959–60	 1960–61
October	—	4.5 (15–25)	—
November	—	2.2 (15–25)	1.9 (18–26)
December	0.8 (18–25)	156.6 (18–33)	69.3 (21–34)
January	0.5 (25)	428.8 (14–31)	66.0 (21–32)
February	1.0 (24–26)	441.1 (14–31)	—
March	153.6 (17–28)	47.9 (15–32)	0.7 (21–26)
April	34.5 (19–32)	40.8 (17–31)	2.3 (19–33)
May	1.7 (31–40)[1]	6.0 (21–43)[1]	8.6 (23–32)

[1] Menhaden more than 34 mm, fork length, are transforming into juveniles; 4 were taken in May 1959 and 14 in May 1960.

On the basis of these field observations, the effects of different low temperatures on larval Atlantic menhaden for various initial or acclimation temperatures were tested in the laboratory (Lewis, 1965). Larvae were acclimated at five temperatures from 7.0 to 20.0 C and were exposed to temperatures from 0.0 to 6.0 C at half-degree intervals. Salinities were held at 24‰ during the tests. The results are briefly, as follows:

> If the test temperature reached 3 C or less, 50 per cent of the larvae died within 1½ days.
>
> If the acclimation temperature was 10 C or warmer, a greater number died at 3 C and 50 per cent were killed at 4.5 C.
>
> Cooling to 1.5 C for less than 12 hours was tolerated by most of the larvae if the acclimation temperatures were below 15 C.

These results indicated that larval menhaden can suffer mass mortalities when water temperatures fall below 3 C for several days or chill rapidly to 4.5 C.

Salinity

Young and adult menhaden tolerate a wide range of salinities, from the fresh water of coastal rivers to high-salinity lagoons (Hildebrand, 1948; Reid, 1955; Gunter, 1956; Breuer, 1957; Simmons, 1957; Gunter and Christmas, 1960). Atlantic menhaden larvae migrate from the ocean where the salinities range from 33 to 36‰ into tributaries near

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[2] Catches of postlarval Atlantic menhaden, *Brevoortia tyrannus*, at Indian River, Delaware. Unpublished manuscript by Anthony L. Pacheco.

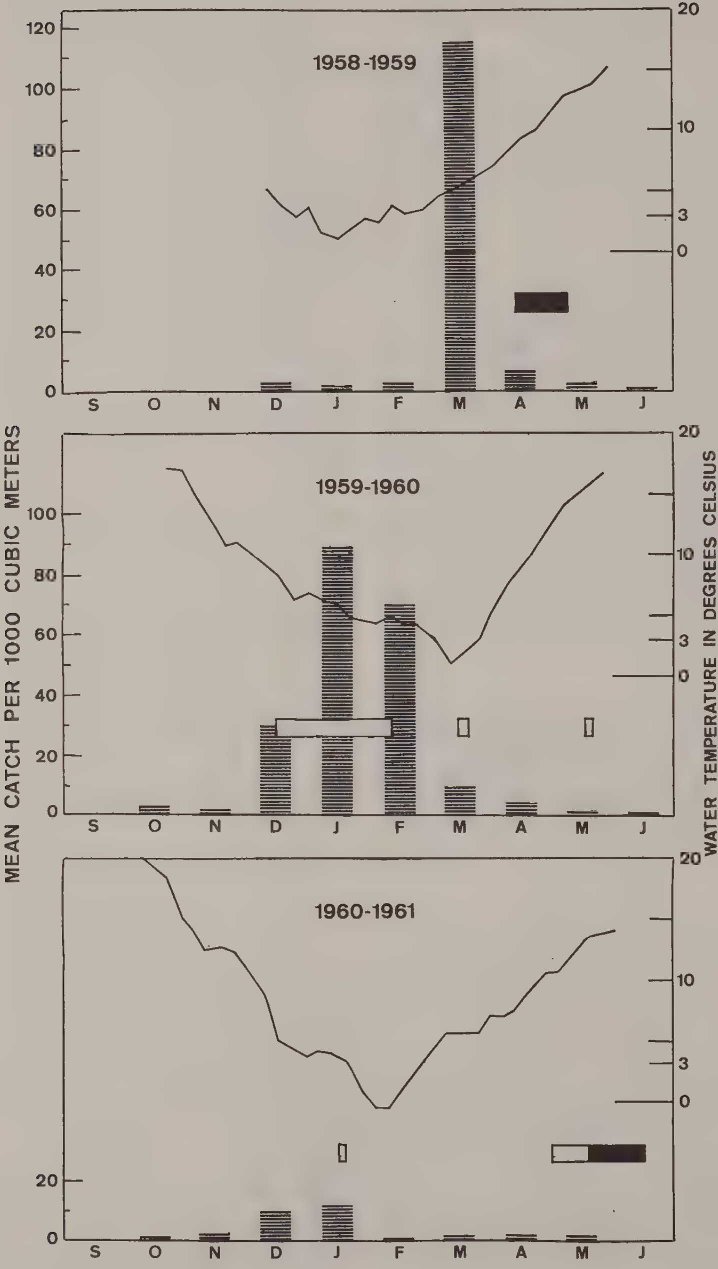

FIGURE 2.—Catches of menhaden larvae and water temperatures in the inlet compared to catches of larvae in a tributary, by month, Indian River, Delaware, 1958–61. The vertical bars represent monthly weighted geometric mean catches of larvae at the inlet during night flood tides. The horizontal bars represent weekly catches at the nursery area (open for 1 to 10 and solid for more than 10). The line graph shows the weekly mean water temperatures at the inlet during flood tides (from Pacheco MS).

the boundary of fresh and salt water where the salinity falls to 1‰ or less (Massmann, Ladd, and McCutcheon, 1954; June and Chamberlin, 1959; Pacheco and Grant, 1965). This tolerance was demonstrated when juvenile menhaden became landlocked in a freshwater reservoir in South Carolina and survived several years to grow to a large size; they gave no evidence of reproduction, however (R. L. Stevens, personal communication).

Mass movements of larvae from the ocean to estuaries for subsequent transformation and growth led to the speculation that lower salinities were required for metamorphosis (June and Chamberlin, 1959). No transforming menhaden were encountered at sea, but larvae undergoing metamorphosis were in tributaries of lower salinities. In 1962 and 1964 however, larvae kept in the laboratory at Beaufort, N. C., completed metamorphosis in salinities at 25 to 40‰. These results indicated that low salinities may not be essential for transformation as was previously thought. Dissection and X-ray examination of the juveniles showed none of the deformities that appeared in the earlier attempt to hold larvae in the laboratory at normal ocean salinities (June and Chamberlin, ibid.).

Observations of menhaden in hypersaline estuaries are limited to the Laguna Madre of Texas where both *B. patronus* and *B. gunteri* were regularly taken in salinities from 20 to 60‰, but rarely above (Simmons, 1957). Simmons also reported mass mortalities, apparently due to salinities of 80‰ or greater. Salinities exceeding 36‰ are rare in Atlantic coast estuaries, and we have no observations or reports of tolerances to high salinity by Atlantic menhaden.

OTHER FACTORS AFFECTING MENHADEN

Many other factors in the environment in addition to temperature and salinity undoubtedly affect the behavior and well-being of menhaden. Some physical factors are light, tides, waves, currents, and turbidity. Light is needed for food production and vision. Tides, waves, currents, and turbidity can influence the suitability of the habitat, as well as the distribution of fish and their feeding. Some of the chemical factors are oxygen, carbon dioxide, hydrogen sulfide, hydrogen-ion concentration, inorganic salts, and organic compounds. Mass mortalities of menhaden have been attributed to oxygen depletion but the suspicion was not confirmed. Generally, no published information is available concerning the effects of physical and chemical factors on Atlantic menhaden.

Food is probably the principal biological factor affecting the well-being of menhaden in an estuary. Zooplankton is the principal food of larval menhaden. During metamorphosis their feeding changes from selective predation upon individual animals to indiscriminant filter-feeding, and their food becomes predominantly diatoms and dinoflagellates with some smaller zooplankters.[3] Their complex branchial filtering apparatus seems capable of retaining nannoplankton, including bacteria. A description of this structure by Monod (1961) supports this view. Peck (1894), who described the food and feeding of juvenile and adult Atlantic menhaden, concluded that their planktonic food had the same species composition as the natural plankton except for the larger and more agile organisms. According to Darnell (1958, 1961), juvenile Gulf menhaden feed on phytoplankton, small crustaceans, and detritus and do some grazing directly upon *Anabaena*, a dense floating scum in Lake Pontchartrain, Louisiana. Menhaden may feed on the bottom as is shown by the presence of detritus, sand, mud, clay, and benthic diatoms (Peck, 1894; Anderson, Jonas, and Odum, 1958).

Crowding sufficient to produce intense competition for space or for food and dissolved oxygen either among menhaden or with other species may restrict populations significantly in the limited nursery areas of many estuaries. Menhaden school from the time of entry into the estuary as larvae, and school size varies with fish size, turbidity, turbulence, and other factors, including predation. The number of schools in an estuary apparently is determined by the suitability of the estuary and by the year-class abundance.

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[3] Food and feeding habits of Atlantic menhaden in relation to the metamorphosis from larval to post-larval stages. Unpublished manuscript by Fred C. June and Frank T. Carlson, U. S. Fish and Wildlife Service, Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N. C.

Juvenile menhaden are preyed upon by many marine carnivores. Some authors (Goode, 1879; Ellison, 1951; Bigelow and Schroeder, 1953) were impressed by the importance of young menhaden as a food for other fishes, but the effects of predation upon the menhaden populations are not known. The principal carnivores reported are bluefish, *Pomatomus saltatrix* (Goode, 1879; Hildebrand and Schroeder, 1928; Ellison, 1951; Bigelow and Schroeder, 1953; Grant, 1962), striped bass, *Roccus saxatilis* (Merriman, 1937; Hollis, 1952), bluefin tuna, *Thunnus thynnus* (Crane, 1936), and sharks (Field, 1907; Bigelow and Schroeder, 1953).

Parasites and diseases are among the more obvious biological factors affecting menhaden, but their role is not well known. Adult Atlantic menhaden often are heavily parasitized by copepods on the body surface and gills (Wilson, 1905, 1915, 1917, 1922, 1932), by monogenetic trematodes on the gills (McMahon, 1963), by digenetic trematodes in the intestine (Linton, 1901, 1905, 1940), by isopods in the buccal cavity (Richardson, 1905), and by sporozoans in the testes (Hardcastle, 1944). Apparently infestation originates, or at least the parasites become noticeable, during the estuarine phase of the life history. Westman and Nigrelli (1955) stated, "Parasites, especially those found on the gills, may contribute to an early demise of fish whose resistance has been considerably reduced by abnormal conditions of the environment such as high temperatures, lowered salinity and other chemical and physical factors leading to an 'imbalance' of the biocenose." Hardcastle (1944) found more than 50 per cent of testes infested with a sporozoan. He stated that the extensive infection could cause sterility. That mass mortalities may be attributable to diseases has been suggested by Westman and Nigrelli (1955). They reported, "The annual, heavy mortality of menhaden in the waters adjacent to New York Harbor occurs in late May and June when millions of fish die and litter the beaches. Dying fish, called 'spinners', are characterized by a loss of coordinated movements and exophthalmia of one or both eyes. Hemorrhages, caused by gas emboli, were noted in the capillaries of the gills, eyes, and optic lobes of the brain. The culture tests of the scales, and the feeding of stomachs and intestines to experimental cats, yielded negative results."

Estuaries apparently are an important habitat for young menhaden. The physical, chemical, and biological factors of this environment affect and in some way determine the populations of menhaden. The number and size of Atlantic and Gulf coast estuaries and the suitability for menhaden are of vital importance to the resource.

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PARALIPARIS WILSONI, A NEW LIPARID FISH FROM THE GULF OF GUINEA

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During a bottom trawling survey carried out from the U. S. Bureau of Commercial Fisheries R/V GERONIMO, off Gabon, West Africa, in September 1963, a fish specimen was caught which represents a new species in the family Liparidae.

Paraliparis wilsoni new species

Holotype: United States National Museum no. 198201, a female, 215.0 mm, standard length, caught off Gabon, West Africa, in a 40-foot shrimp trawl from the U. S. Bureau of Commercial Fisheries R/V GERONIMO cruise 2, station 240, 04°08′S–010°08′E; depth 1134 meters; 9 September 1963.

Diagnosis: A *Paraliparis* with simple teeth in a single series, 24 pectoral rays, and many rudimentary pores extending posteriorly in a single line along the body behind the single suprabranchial pore.

Counts and measurements: The measurements are in millimeters, and percentages of standard length are in parentheses. The counts of vertebrae, dorsal fin rays, anal fin rays, and caudal fin rays are from radiographs. Greatest body depth 47.6 (22.1); body width at level of anal fin origin 15.4 (7.2); greatest head width 29.5 (13.7); head length 36.4 (16.9); eye 8.9 (4.1); snout length 12.3 (5.7); interorbital width 16.5 (7.7); gill slit 6.1 (2.8); snout to posterior tip of pectoral fin 62.0 (28.8); length of upper lobe of pectoral fin 21.0 (9.8); length of lower lobe of pectoral fin 8.3 (3.9); snout to anus 39.0 (18.1); dorsal rays 63; anal rays 56; pectoral rays 24; caudal rays 8; vertebrae $12 + 58 = 70$, including hypural; branchiostegals 6; abdominal caecae 6, all on left side; cephalic pores include 2 on snout, 6 in a series extending along lower margin of snout and curving dorsally to above and behind the eye, and 7 in a series extending from tip of lower jaw to opercle; 1 suprabranchial pore above the gill slit.

Description: A moderately slender and compressed fish with greatest body depth (just behind head) 4.5 in standard length; body width at

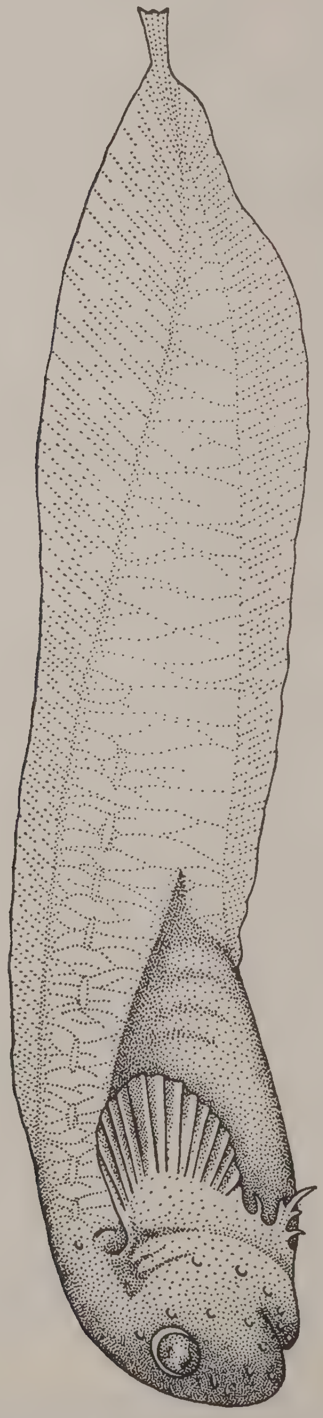

Fig. 1. Holotype of *Paraliparis wilsoni*, 215.0 mm in standard length. Drawn by Lorraine Pilon Sund.

level of anal fin origin, 14.0 in standard length. Skin smooth, lacking prickles, and very loose on body and fins.

Dorsal fin origin a short distance behind vertical from gill slit; dorsal fin unnotched, height increasing from origin, and highest at about fin rays 43–50. Anal fin origin at posterior end of abdominal cavity, at a distance from vent of 4.1 in standard length. Pectoral fin deeply notched; nineteenth ray, counting dorsal to ventral at apex of notch.

Head slightly deeper than broad in opercular region. Snout protruding over the inferior mouth; snout length 3.0 in head. Eye large, 4.1 in head; pupil round. Nostril single and oval without a flap, resembling a cephalic pore, and located midway between posterior snout pore and anterior edge of eye. At least 10 rudimentary pores extend posteriorly on body from suprabranchial pore. Very small simple teeth form a row on the premaxillary and dentary bones, but are absent at the premaxillary symphysis. Prevomerine and palatine teeth not discernible. Gillrakers not discernible. Gill opening small, 6.0 in head, and located directly above pectoral fin base.

Skin semi-transparent and covered with many small brown chromatophores. Chromatophores arranged in a diffuse, vertically oriented pattern on body; concentrated on anterior part of head and on fin edges, giving these areas a dark appearance. Eye, interior of mouth, gill cavity, gill slit, peritoneum, vent, strip posterior to vent on abdominal cavity, and rectal portion of gut black. Dorsal outline of abdominal cavity black, with black streaks curving anteroventrally. Body has a few irregular black spots, particularly near region of abdominal cavity. Gut white, except in rectal area.

Relationships: The genera *Careproctus* Kroyer and *Paraliparis* Collett are very similar in many characters (Burke, 1930). The presence of a ventral disk and rudimentary pores in *Careproctus* and their absence in *Paraliparis* are the two most important distinguishing characters. However, *P. wilsoni*, while lacking any vestige of a ventral disk, does have rudimentary pores on the body. Therefore, the generic allocation of this species is tentative.

If *P. wilsoni* is correctly placed in *Paraliparis*, then its closest relative is probably *P. copei* Goode and Bean, the only other Atlantic species with simple teeth in a single series. The single specimen of *P. wilsoni* differs from *P. copei* in having: rudimentary pores on the body posterior to the suprabranchial pore (none on *P. copei*); more pectoral rays (21–22 in *P. copei*); and a different color pattern (*P. wilsoni* is very dark and has a distinct chromatophore pattern, whereas *P. copei* is light, except on the snout and fin edges, and has no recognizable chromatophore pattern). No reliable distinction between *P. wilsoni* and *P. copei* is apparent in the numbers of dorsal rays, anal rays, or vertebrae (the numbers in *P. copei* are, respectively: 61–64, 57–60, and 68–71).

Specimens of P. copei examined: U. S. 35637, the holotype, 160.9 mm in standard length, collected at R/V ALBATROSS station 2232, 39°12′17″N–072°09′30″W; depth 520 fathoms; 13 September 1884.

U. S. 186151, 139.4 mm in standard length, collected at R/V DELAWARE station 59–10, 39°47′N–070°57′W; depth 800 fathoms; 27 August 1959.

Acknowledgments: Dr. Daniel M. Cohen, U. S. Bureau of Commercial Fisheries, provided much advice as well as the X-rays of *P. wilsoni* and of the two specimens of *P. copei* examined. He also critically read the manuscript. Mr. J. Blache, Museum National d'Histoire Naturelle, Paris, France, made several valuable suggestions.

P. wilsoni is named for Mr. Robert C. Wilson, U. S. Bureau of Commercial Fisheries, who conceived and directed the trawling survey during which this new species was collected.

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Systematics of the Percid Fishes of the *Etheostoma thalassinum* Species Group with Comments on the Subgenus *Etheostoma*[1]

WILLIAM J. RICHARDS[2]

The subgenus *Etheostoma* is diagnosed and redescribed, and relationships of the species within this subgenus are discussed. *Etheostoma thalassinum* from the Santee River System and *E. inscriptum* from the Altamaha, Savannah, and Edisto river systems are shown to be closely related. *E. swannanoa*, from the headwaters of the Tennessee River system, exhibits several specialized features: absence of palatine teeth, reduction in number of prevomerine teeth, and presence of a basal orange-red band in the spinous dorsal fin. These features among others relate this group to *E. blennioides*.

INTRODUCTION

THE object of this study was to examine infraspecific variation and to clarify the interspecific relationships of *Etheostoma thalassinum* (Jordan and Brayton), *E. inscriptum* (Jordan and Brayton), and *E. swannanoa* Jordan and Evermann. These species are allopatric in the southeastern United States and are members of the subgenus *Etheostoma* Rafinesque. Necessary aspects of the study have been to diagnose, redescribe, and discuss the species-group relationships in the subgenus *Etheostoma*.

Counts and measurements were made according to the methods described by Hubbs and Lagler (1958), except for diagonal or transverse scale counts which follow Bailey's method (1959), and trans-pelvic width measurements which follow the Bailey and Richards method (1963).

The subgenus *Etheostoma* is most closely related to the subgenus *Ulocentra. Ulocentra* shows more loss of structures than *Etheostoma* and thus is more specialized, although species of *Etheostoma* approach *Ulocentra* closely in this respect. Unfortunately most of the species of *Ulocentra* are as yet undescribed. Therefore their diagnostic separation cannot at present be entirely satisfactory. The characters which usually distinguish *Ulocentra* from *Etheostoma* are the following: steeply declivous snout with frenum absent or slightly developed; lack of breeding tubercles; usually five branchiostegals; usually eight or nine dorsal blotches; and more red on the fins and body (species of *Etheostoma* usually have more green). The other subgenera of *Etheostoma* are easily separable from the above: *Boleosoma* has one or two thin flexible anal spines; *Ioa* has a translucent body and fleshy villi encircling the anus; *Austroperca* and *Psychromaster*, though not closely related, have a single thick inflexible anal spine (occasional individuals have two), *Nothonotus, Allohistium, Oligocephalus,* and *Villora,* which apparently are closely related to one another, have closely approximated pelvic fins, branchiostegal membranes usually separate or only moderately conjoined, and snout produced and sharp (not declivous); *Catonotus*, which is probably related to the four preceding subgenera, has interrupted supratemporal and infraorbital canals; *Hololepis* has a highly arched lateral line; and *Microperca* has only from six to eight preoperculomandibular pores.

The relationships of the species within the subgenus *Etheostoma* have never been discussed in their entirety. Hubbs and Black (1940) gave a full treatment of the relationships of the *E. variatum* (Kirtland) species group and also pointed out some of the salient features of *E. sellare* (Radcliffe and Welsh). Bailey and Gosline (1955:16, 39–40) included 15 species in the subgenus *Etheostoma*. (*E. gutselli* (Hildebrand) is now regarded as a subspecies of *E. blennioides* by Miller (1965), an opinion in which I concur.) I include the same species in the subgenus and among them recognize three species groups. The members of these groups are:

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[1] This contribution is part of a thesis submitted to the Graduate Faculty of Cornell University in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] Contribution No. 36, Bureau of Commercial Fisheries Tropical Atlantic Biological Laboratory, Miami, Florida.

variatum group

- *E. variatum* Kirtland
- *E. osburni* (Hubbs and Trautman)
- *E. tetrazonum* (Hubbs and Black)
- *E. euzonum* (Hubbs and Black)
- *E. kanawhae* (Raney)

Specialized relatives:

- *E. blennius* (Gilbert and Swain)
- *E. sellare* (Radcliffe and Welsh)

thalassinum group

- *E. thalassinum*
- *E. inscriptum*
- *E. swannanoa*

blennioides group

- *E. blennioides* Rafinesque
- *E. zonale* (Cope)
- *E. rupestre* Gilbert
- *E. histrio* (Jordan and Gilbert)

SUBGENUS *ETHEOSTOMA* RAFINESQUE

Etheostoma Rafinesque, 1819:419. Type species, *Etheostoma blennioides* Rafinesque, by subsequent designation of Agassiz, 1854:304–305, as stated in Opinion 14, International Commission Zoological Nomenclature 1910:25–27. Bailey and Gosline, 1955:1–44. Generic and subgeneric names listed.

Diplesion Rafinesque, 1820:37. Type species, *Etheostoma blennioides* Rafinesque, by subsequent designation of Jordan and Evermann. 1896:1052.

Poecilosoma Agassiz, 1850:299. Type species, *Etheostoma variata* Kirtland, by original designation.

Poecilichthys Agassiz, 1854:305. Type species, *Etheostoma variata* Kirtland, by original designation. Substitute name for *Poecilosoma* Agassiz, preoccupied by *Poecilosoma* Huebner, 1819, in Lepidoptera.

Hyostoma Agassiz, 1854:305. Type species, *Hyostoma newmanii* Agassiz [= *E. blennioides*], by original designation.

Nanostoma Putnam, in Jordan, 1877:6. Type species, *Poecilichthys zonalis* Cope, by subsequent designation of Jordan, 1877:7.

Rhothoeca Jordan, 1885:80. Type species, *Poecilichthys zonalis* Cope, by original designation. Substitute name for *Nanostoma* Putnam, erroneously regarded as preoccupied by *Nannostomus* Günther, 1872, in Pisces.

Diagnosis.—A subgenus of the genus *Etheostoma* with: lateral line straight and complete; cephalic canals complete; body opaque; two anal spines, the first heavy and stiff; pelvic fins widely spaced; branchiostegal membranes connected; snout declivous; and dark dorsal saddles or blotches on body, usually numbering from four to seven.

Description.—Preoperculomandibular pores 10 (8 or 9 in some populations of *E. zonale* and *E. histrio*); prevomer with teeth or edentulous; palatine with teeth or edentulous; branchiostegal membranes broadly conjoined (only slightly conjoined in *E. sellare*); branchiostegal rays 6, occasionally 5; preopercle entire; top of head scaleless; cheek, opercle, nape, prepectoral area, breast, and belly variably scaled or naked; body scales large to small (scales in the lateral series 39 to 78); body rather elongate, slightly compressed; head of moderate length; vertebrae 37 to 44; snout blunt to produced; premaxillary frenum well developed to absent; mouth horizontal, inferior, and usually small; interorbital area broad to narrow; dorsal fin rays (rarely VIII) IX to XIV—10 to 15; anal fin rays II, 8 to 11; pectoral fin rays 13 to 17; fins large and expanded, spines of first dorsal fin without fleshy tips; pelvic fins well separated, transpelvic width 8.0–11.1% of standard length; anus not encircled with fleshy villi; breeding tubercles present or absent on ventral body scales of males and females; genital papilla of female long and tubular except in *E. sellare*; sexual dimorphism well marked in most species, males usually brightly colored, green predominant; dorsum with 4–7 well developed saddles or 6–7 well developed blotches. These fish are small to large darters which inhabit riffles with a substrate of fine gravel to large boulders. The species are widely distributed throughout the Mississippi River basin and the Gulf of Mexico drainages from the Mississippi River to Mobile Bay; they are discontinuously distributed in Atlantic drainages from the Altamaha River basin, the Santee River basin, the headwaters of the Potamac River, Swan Creek at the head of Chesapeake Bay, and the Mohawk-Hudson River basin; and in the Great Lakes basin eastward in the southern tributaries of Lake Ontario.

Evolutionary relationships.—One of the best indicators of the interrelationships of these species is the condition of the prevomerine and the palatine teeth. In all of the other

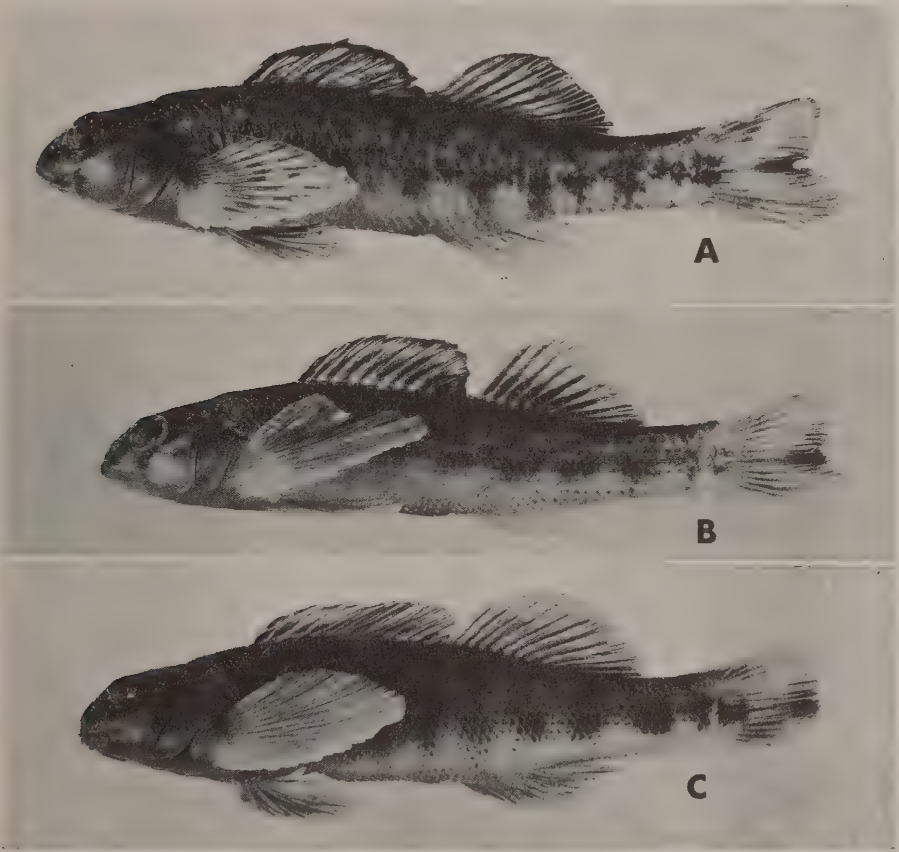

Fig. 1. Male breeding patterns. A. *Etheostoma thalassinum*; CU 10906; 55 mm; McDowell Co., N. C., Santee Dr.; 7 April 1947. B. *E. inscriptum*; CU 10932; 50 mm; Ga., Hall Co., Altamaha Dr.; 9 April 1947. C. *E. swannanoa*; CU 41842; 64 mm; Smyth Co., Va., Holston Dr.; 2 April 1962.

species of the genus *Etheostoma*, no variation occurs among the species within a subgenus —except for *Ulocentra* wherein palatine teeth are always absent but there is some variation between species in the absence or presence of prevomerine teeth. I have examined specimens of all described darters and have found both palatine and prevomerine teeth present in *Boleosoma, Nothonotus, Oligocephalus, Villora, Catonotus, Psychromaster, Austroperca, Hololepis,* and *Microperca*; palatine teeth absent and prevomerine teeth present in *Allohistium*; and both palatine and prevomerine teeth absent in *Ioa*. Variation in the presence and absence of both prevomerine and palatine teeth does occur among the species within the subgenus *Etheostoma*. This variation may be an indicator of interrelationships. The *variatum* group has both prevomerine and palatine teeth. The color pattern within this group is almost constant: bright green, blue, and red form a predominant candy-stripe pattern on breeding males. The spinous dorsal fin has a marginal red band. Further, the breeding males and females have an extensive development of breeding tubercles on the ventral body scales (refer to Collette, 1965 for additional data on breeding tubercles). The dorsal blotches number 4–6 and extend down over the sides as saddles.

E. blennius was placed in the *variatum* group by Hubbs and Black (1940), but it

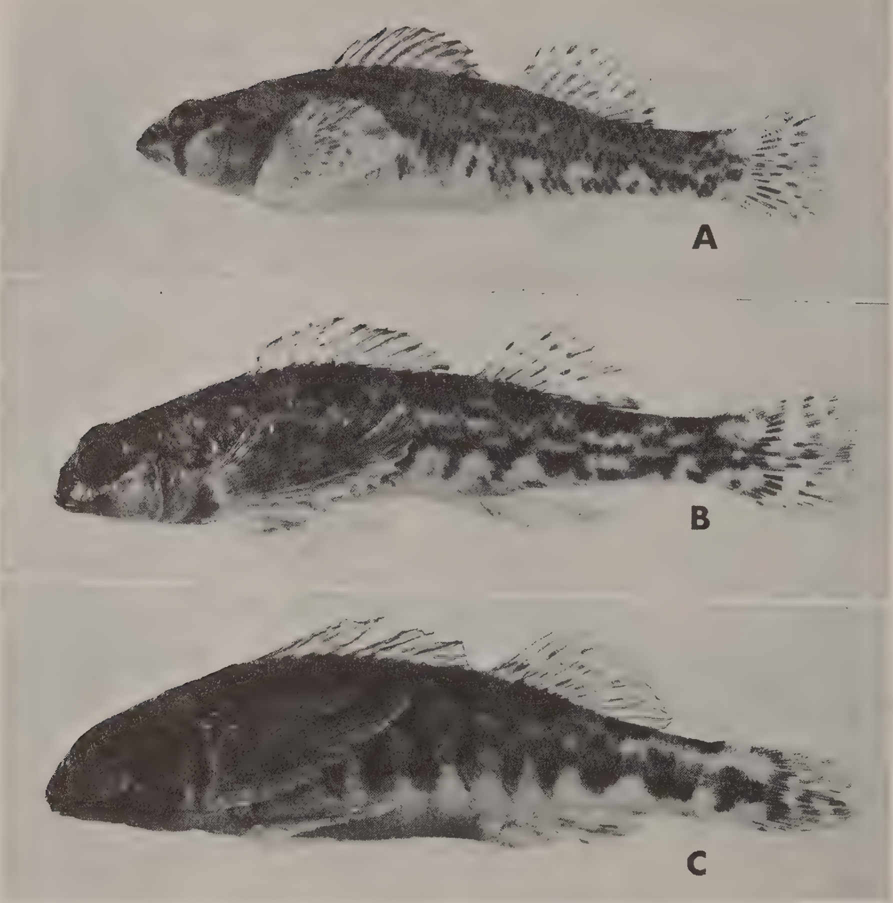

Fig. 2. Female breeding patterns. A. *Etheostoma thalassinum*; CU 10920; 45 mm; Greenville Co., S. C., Santee Dr.; 7 April 1947. B. *E. inscriptum*; CU 38136; 56 mm; Pickens Co., S. C., Savannah Dr.; 3 June 1961. C. *E. swannanoa*; CU 37632; 56 mm; Cocke Co., Tenn., Tennessee Dr.; 29 March 1961.

differs in the lack of palatine teeth, breeding tubercles (none found by Collette, 1965, or me), and the distinctive candy-stripe color pattern. It also has four dorsal saddles which are more developed than the *variatum* type and most closely resemble those in *E. sellare*. Furthermore, *E. blennius* has a small, inferior mouth and a declivous snout. Hubbs and Black (1940:3, 6–9) pointed out several other distinctive characteristics. *E. blennius* is probably a specialized relative of the *variatum* group.

E. sellare remains an enigma because no adult males have been reported (Knapp, *et al.*, 1963). *E. sellare* has both prevomerine and palatine teeth. Its dorsal saddles most closely resemble those of *E. blennius*. The snout is produced and, in lateral profile, the head is depressed. The head has a distinctive triangular shape when viewed from above (see plate 18, Radcliffe and Welsh, 1913). The genital papilla is unusual; it was described by Hubbs and Black (1940:3). The branchiostegal membranes are only slightly connected, but since this character seems to be variable within species and species groups (i.e., species of *Catonotus* and *Oligocephalus*), its value is debatable. No other darter even slightly resembling *E. sellare* lives within 200 miles of Swan Creek. *E. sellare* may represent a primitive relict species of the subgenus *Etheostoma* related most closely to *E. blennius* and in turn to the *variatum* group. (I have examined recent collections of *E. sellare* which include adult males. These specimens do not alter my conclusions.)

In the *thalassinum* group the number of prevomerine and palatine teeth is reduced; in *E. swannanoa* and some populations of *E. inscriptum*, palatine teeth are absent. The dorsal pattern is made up of six or seven blotches rather than saddles. Breeding tubercles are present only on the ventral body scales in males. The color pattern is predominantly solid green, not vertically barred. A narrow marginal red band is present on the spinous dorsal fin (*E. blennius*, of the *variatum* group, has a similar band). In this species group, *E. swannanoa* is unique in having an orange basal band in the spinous dorsal fin. This basal band suggests relationship to the *blennioides* group. (The *thalassinum* group was referred to as the *inscriptum* group by Collette, 1965.)

In the *blennioides* group, palatine teeth are absent and prevomerine teeth are consistently present only in *E. zonale* and *E. histrio* in reduced numbers. Prevomerine teeth are rarely present in *E. blennioides*, and in only about 50% of specimens of *E. b. gutselli* and *E. rupestre*. Breeding tubercles are absent except in males of *E. blennioides* and *E. b. gutselli* (Collette, 1965). The dorsum has six or seven blotches, as in the *thalassinum* group. Green, the predominant color, occurs as bright bars on the sides of the body particularly in breeding males. None of the group has a marginal red band on the spinous dorsal fin, but all have a red basal bar on this fin. The premaxillary frenum (well developed in the other two species groups) is only slightly developed or absent. The number of branchiostegal rays is usually 6, but 5 is not unusual in populations of some species—particularly *E. zonale*. The presence of many of these features in the subgenus *Ulocentra* suggests close relationship.

In summary, these species group relationships are based on the presence or absence of prevomerine and palatine teeth, distribution of breeding tubercles, general body shape,

TABLE 1. SCALE COUNTS IN *Etheostoma thalassinum*, *E. inscriptum*, AND *E. swannanoa*.

	Lateral-Line Scales																										
Species	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	n	x̄
E. thalassinum	2	12	38	53	61	35	32	27	13	5	4	–	1	–	–	–	–	–	–	–	–	–	–	–	–	283	42.41
E. inscriptum	–	1	–	2	8	20	49	69	104	139	161	160	111	94	47	36	4	4	3	–	1	–	–	1	–	1014	48.21
E. swannanoa	–	–	–	–	–	–	–	–	1	4	14	9	21	25	35	32	32	28	20	23	17	10	6	1	2	280	53.60

	Transverse Scales																									
	Above Lateral Line								Below Lateral Line							Total										
	4	5	6	7	8	9	n	x̄	4	5	6	7	8	n	x̄	9	10	11	12	13	14	15	16	17	n	x̄
E. thalassinum	2	201	76	5	–	–	284	5.30	11	242	30	1	–	284	5.07	1	9	180	73	19	2	–	–	–	284	11.37
E. inscriptum	1	28	156	10	–	–	195	5.90	1	82	108	4	–	195	5.59	–	2	22	63	97	10	1	–	–	195	12.48
E. swannanoa	–	–	19	56	36	4	115	7.22	–	15	60	25	11	111	6.29	–	–	–	12	8	43	20	20	6	109	14.42

	Least Caudal Peduncle Scales																												
	Above Lateral Line								Below Lateral Line								Total												
	5	6	7	8	9	10	n	x̄	6	7	8	9	10	11	n	x̄	13	14	15	16	17	18	19	20	21	22	23	n	x
E. thalassinum	15	127	32	–	–	–	174	6.10	21	148	5	–	–	–	174	6.91	3	24	114	27	6	–	–	–	–	–	–	174	15.05
E. inscriptum	3	43	148	7	–	–	201	6.79	3	76	81	21	–	–	181	7.66	1	4	9	56	89	11	4	–	–	–	–	175	16.58
E. swannanoa	–	2	26	44	38	2	112	8.11	1	3	15	43	37	13	112	9.35	–	–	2	4	10	14	23	23	25	10	1	112	19.47

Table 2. Dorsal, Anal, and Pectoral Fin-ray Counts in *Etheostoma thalassinum*, *E. inscriptum*, and *E. swannanoa*.

Dorsal Spines

Species	8	9	10	11	12	13	n	$\bar{x}$
E. thalassinum	1	44	174	37	–	–	256	9.96
E. inscriptum	7	129	494	67	3	–	700	9.90
E. swannanoa	–	–	1	29	80	23	133	11.94

Dorsal Soft Rays

	9	10	11	12	13	14	n	$\bar{x}$
E. thalassinum	–	4	94	142	17	–	257	11.67
E. inscriptum	2	43	360	301	13	–	719	11.39
E. swannanoa	–	–	11	58	51	2	122	12.36

Total Dorsal Rays

	18	19	20	21	22	23	24	25	26	n	$\bar{x}$
E. thalassinum	–	1	20	86	116	31	2	–	–	256	21.63
E. inscriptum	3	10	104	307	230	35	4	–	–	693	21.26
E. swannanoa	–	–	–	–	5	15	51	39	13	123	24.33

Anal Rays

	II, 6	II, 7	II, 8	II, 9	II, 10	n	$\bar{x}$
E. thalassinum	1	16	171	95	3	286	8.29
E. inscriptum	1	138	498	67	1	705	7.90
E. swannanoa	–	7	69	28	–	104	8.20

Total Pectoral Rays

	26	27	28	29	30	31	32	33	34	n	$\bar{x}$
E. thalassinum	15	21	159	36	40	2	1	–	–	274	28.27
E. inscriptum	23	31	390	89	153	4	3	–	–	693	28.49
E. swannanoa	–	–	–	5	33	24	52	8	2	124	31.25

color pattern, and habits. I believe that the presence of both palatine and prevomerine teeth, and breeding tubercles in both sexes, represents a primitive condition in these fishes. The presence in the *variatum* group of palatine and prevomerine teeth and breeding tubercles in both the males and females indicates that group to be the most primitive in the subgenus *Etheostoma*. The *thalassinum* species group is slightly more specialized, to the extent that it shows losses in dentition and of breeding tubercles in females. The most specialized of the three is the *blennioides* group, as shown by the absence of palatine teeth in both sexes, the absence or reduction of prevomerine teeth, and the absence of breeding tubercles in females of all species and in males of three of the five species.

Etheostoma thalassinum group.—The three species in this group are closely related and difficult to separate. *E. swannanoa* is the most distinct and exhibits the most specialized features, particularly a reduction in dentition. *E. thalassinum* and *E. inscriptum* may be separated by three pigmentation characters. *E. thalassinum* has 7 dorsal blotches (rarely 6) whereas *E. inscriptum* and *E. swannanoa* each have 6 (rarely 5). In life, the body scales of males of *E. inscriptum* and *E. swannanoa* have red centers, giving an appearance of horizontal red lines (dark lines and spots in preserved specimens). Males of *E. thalassinum* have weakly developed red spots which are seldom visible as lines or dark spots in preserved specimens. *E. inscriptum* males have red on the head; this is reduced or absent in *E. thalassinum*. On the body and caudal peduncle of males of *E. thalassinum* are dark vertical bars which usually extend to the anal-fin base and onto the belly. In males of *E. inscriptum* these bars extend only a few scale rows below the lateral line. In this character, *E. swannanoa* is like *E. inscriptum*. The males of *E. swannanoa* have an orange band on the base of the spinous dorsal fin. The females of these species are very difficult to separate.

(Meristic data for the three species are given in Tables 1–3 and geographic distributions are given in Fig. 4.)

The following hypothesis for the dispersal and evolution of the group is suggested on the basis of the relationships among the species, their geographic distribution, and the drainage topography in their region of occurrence. *E. thalassinum* is the most primitive of the three species because of the greater abundance of both prevomerine and palatine teeth, and the presence of seven dorsal blotches. (1) Its ancestor probably reached the Santee River basin from the Mississippi River basin through headwater stream piracy of the Tennessee River. (2) Its ancestor later reached the Savannah River, differentiating into an *E. inscriptum* ancestor. (3) *E. inscriptum* subsequently spread southward to the Altamaha and Edisto drainages, becoming slightly differentiated there. (The migration to the Altamaha was probably by stream capture in the Piedmont region, and to the Edisto by Coastal Plain flooding.) (4) The ancestor of *E. inscriptum* then spread westward across the mountains to the Tennessee River basin, differentiating into present-day *E. swannanoa*.

An alternative explanation is that *E. swannanoa* arose directly from the *E. thalassinum* ancestor and exhibits several evolutionary parallels with *E. inscriptum*. Specializations common to *E. inscriptum* and *E. swannanoa* are the loss of the last dorsal blotch, loss of palatine teeth in some populations, development of a high degree of sexual dichromatism of males, and enlarged genital papilla in the females (of *E. swannanoa*). In *E. swannanoa*, the brown coloration in place of the green of *E. thalassinum* and *E. inscriptum*, indicates that a derivation from *E. swannanoa* could not be logically hypothesized.

Variation with sex and year-classes.—A study was made on several meristic characters in three large series of *E. inscriptum* taken at nearly the same time of the year, in different years, from a relatively isolated locality to assess the possible effects of sexual and year-class variation. The characters studied included the number of lateral-line scales and fin rays. Chi-square tests showed no significant differences in the characters studied between fish taken in different years, but significant differences were found between sexes in number of fin rays. In analyzing geographic variation in the *thalassinum* group, fin-ray counts are of little value; therefore, sex does not have to be taken into consideration. Complete data for these tests may be found in Richards (1963).

Ecological considerations.—The three species of this group are all riffle inhabitants. The streams inhabited varied from 5 ft in width to as much as 1200 ft. The water was always colorless but, on several occasions, was turbid as a result of recent storms in the area. The bottom of the riffles contained either sand, gravel, rubble, large boulders, or bedrock, or a combination of these. The depth was usually less than 2 ft. The current was normally moderate; slow and swift currents have been noted on several occasions. Normally, vegetation was absent from these riffles except for algae on rocks at several localities. Water temperatures on dates of collection were 50–60° F in March, 45–68° F in April, 54–74° F in June, and 70° F in September.

Fishes collected in riffles with *E. thalassinum* included the darters *E. flabellare* Rafinesque and *Percina crassa* (Jordan and Brayton), and the madtom, *Noturus insignis* (Richardson). *E. inscriptum* was commonly taken with the darters *Percina nigrofasciata* (Agassiz), *E. hopkinsi hopkinsi* (Fowler), *E. h. binotatum* Bailey and Richards, and *E. fricksium* (Hildebrand); the sculpin *Cottus bairdii* Girard; and the madtoms *Noturus insignis* and *N. leptacanthus* (Jordan). *E. swannanoa* was commonly taken with *Percina evides* (Jordan and Copeland), *E. simoterum* (Cope), *E. flabellare*, and *E. rufilineatum* (Cope). Other species included the sculpins *Cottus carolinae* (Gill), *C. bairdii*, and *C. baileyi* Robins; the minnows *Rhinichthys cataractae* (Valenciennes), and *Campostoma anomalum* (Rafinesque).

Nothing has been published on habits of these fishes, but I found *E. inscriptum* and *E. thalassinum* distributed throughout the various riffles sampled. However, *E. swannanoa* was more specialized in that it was usually confined to the deeper portions of riffles among loose rocks 6 to 10 inches in diameter, with fine gravel interstices. *E. simoterum* and *Cottus carolinae* were commonly taken in this same environment. *E. rufilineatum* was usually found in shallower portions of the riffle (6–8 inches deep) in loose gravel, and *Percina evides* was usually taken deeper in swift runs (2–3 ft deep).

Pairs of *E. swannanoa*, apparently mated,

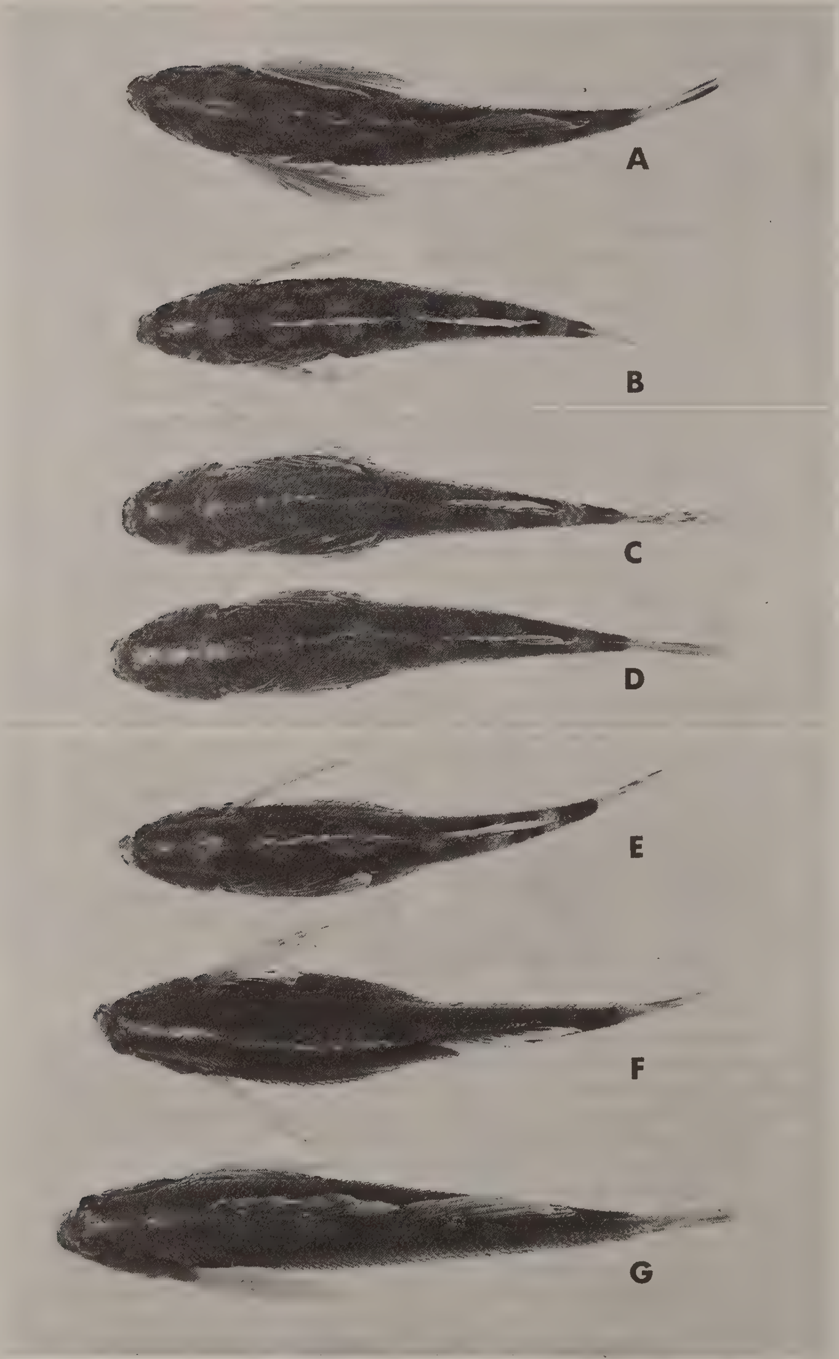
A
B
C
D
E
F
G

TABLE 3. NUMBER OF PREVOMERINE AND PALATINE TEETH IN *Etheostoma thalassinum*, *E. inscriptum*, AND *E. swannanoa* FROM VARIOUS AREAS.

	Prevomerine Teeth																						
Species	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	n	$\bar{x}$
E. thalassinum	–	1	–	2	1	4	4	5	2	1	–	–	–	–	–	–	–	–	–	–	–	20	5.75
E. inscriptum																							
Savannah	1	1	2	4	2	4	10	6	10	10	6	4	4	3	3	1	1	–	1	–	1	74	8.36
Altamaha	–	–	1	4	4	5	9	3	3	1	–	–	–	–	–	–	–	–	–	–	–	30	5.43
Edisto	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	4.00
Total	1	1	3	9	7	10	19	9	13	11	6	4	4	3	3	1	1	–	1	–	1	107	7.42
E. swannanoa	–	–	1	–	4	3	2	3	2	–	–	–	–	–	–	–	–	–	–	–	–	15	5.47

	Left Palatine Teeth									Right Palatine Teeth									
	0	1	2	3	4	5	6	n	$\bar{x}$	0	1	2	3	4	5	6	7	n	$\bar{x}$
E. thalassinum	5	3	9	3	–	–	–	20	1.50	10	4	3	2	–	1	–	–	20	1.05
E. inscriptum																			
Savannah	11	22	18	11	8	3	1	74	1.95	8	18	27	14	5	1	–	1	74	1.97
Altamaha	29	1	–	–	–	–	–	30	0.03	28	2	–	–	–	–	–	–	30	0.07
Edisto	3	–	–	–	–	–	–	3	0	3	–	–	–	–	–	–	–	3	0.00
Total	43	23	18	11	8	3	1	107	1.36	39	20	27	14	5	1	–	1	107	1.38
E. swannanoa	15	–	–	–	–	–	–	15	0	13	2	–	–	–	–	–	–	15	0.13

were consistently taken in the same seine haul on 2 April 1962 in the middle fork of the Holston River at the northern corporate limits of Marion, Smyth County, Virginia. When a small area (6 ft × 6 ft) was "kicked out," a male and female were taken. The males were running milt, and the females could be easily stripped of eggs, but a search revealed no eggs on the substrate. The fish were in the deepest part of the riffle (12–18 inches deep) over a rubble bottom of stones 6–8 inches in diameter and fine gravel. The river was slightly swollen and cold (45.5° F), due to a rain and snow storm the previous day. The water was colorless, but also very turbid because of highway construction nearby.

Etheostoma thalassinum
(Jordan and Brayton)
Seagreen darter

Nothonotus thalassinus Jordan and Brayton, 1878:13 (original description).

Nanostoma thalassinum. Jordan and Gilbert, 1882:511 (description). Jordan, 1929:163 (description; range). Jordan, Evermann, and Clark, 1930:289 (partial synonymy).

Etheostoma (*Rhothoeca*) *thalassinum*. Jordan, 1885:80 (listed).

Etheostoma thalassinum. Jordan, 1888:139 (listed). Boulenger, 1895:83 (in part; description; excluding most of synonymy). Pickens, 1928:31 (distribution). Hubbs and Black, 1940:25 (listed). Bailey and Gosline, 1955:16, 39 (subgeneric allocation, vertebral counts). Moore, 1957:186, 191 (key, characters, range). Anderson and Freeman, 1957:106, 109 (range). Eddy, 1957:215 (key, figure). Richards, 1964:3899 (diss. abstr.).

Etheostoma (*Nanostoma*) *thalassinum*. Jordan and Evermann, 1896:1071–1072 (description, range, partial synonymy).

Poecilichthys thalassinus. Schrenkeisen, 1938: 228 (characters, range).

Types.—Lectotype: USNM 31132 (male, 40 mm SL), Saluda River near Greenville, S. C.,

←

Fig. 3. Dorsal pigment patterns of the subgenus *Etheostoma*. A. *E. thalassinum* ♂; CU 9802; 57 mm; Polk Co., N. C., Santee Dr.; 4 April 1940. B. *E. thalassinum* ♀; CU 9802; 51 mm; same data as A. C. *E. inscriptum* ♂; CU 38136; 58 mm; Pickens Co., S. C., Savannah Dr.; 3 June 1961. D. *E. inscriptum* ♀; CU 38136; 56 mm; same data as C. E. *E. swannanoa* ♀; CU 37632; 56 mm; Cocke Co., Tenn., Tennessee Dr.; 29 March 1961. F. *E. swannanoa* ♀; CU 37629; 60 mm; Smyth Co., Va., Tennessee Dr.; 27 March 1961. G. *E. swannanoa* ♂; CU 41842; 64 mm; Smyth Co., Va., Tennessee Dr.; 2 April 1962.

summer 1877, D. S. Jordan and A. W. Brayton; selected by Jordan and Evermann (1896: 1072). Paralectotypes: SU 987 (female, 46 mm SL; 5 males, 37–49 mm SL), Saluda River at Farr's Mills, W of Greenville, summer 1877, D. S. Jordan, A. W. Brayton. MCZ 24397 (male, 44 mm SL), Saluda River, S. C. The types in the U. S. National Museum were examined by me; those at Stanford University and Harvard University by Collette and Knapp (1966).

Diagnosis.—A species of the subgenus *Etheostoma* with prevomerine teeth and usually with palatine teeth; dorsal blotches 7 (8 of 284 specimens examined with 6 dorsal blotches); premaxillary frenum well developed; marginal red band in spinous dorsal fin; breeding tubercles on ventral scales in breeding males; and branchiostegal membranes broadly connected. Head, cheek, opercle, prepectoral area, and breast naked; nape variably naked to fully scaled, with exposed or embedded ctenoid (rarely cycloid) scales; belly variably partly naked to fully scaled, with exposed ctenoid scales. Body coloration predominantly green, with red weakly developed on body scales. Lateral-line scales (38) 39 to 45 (50). (90% of the specimens examined ranged from 39 to 45. The extremes of all the specimens counted are shown in parentheses.) Vertebrae 39 or 40 (Bailey and Gosline 1955: 16).

Coloration.—The following description is based on both preserved and living specimens. The spinous dorsal fin in both sexes has a narrow white margin (clear in preserved specimens), and below this a submarginal reddish-orange band (brownish in preserved specimens) which is usually wider in males. The remainder of the fin is clear and has irregular concentrations of micromelanophores which are concentrated on the interspinous membranes of the anterior two or three spines and of the posterior one or two spines. These melanophores are more concentrated in males, particularly breeding males. The soft dorsal fin in males is clear except for brown spots on the basal portion of the interradial membranes. Females have this same pattern but, in addition, have patches of brown on the anterior and posterior edges of the rays, which give an appearance of banding to the fin (Figs. 1 and 2). The caudal fin is patterned like the soft dorsal, with brown spots on the base of the interradial membranes in males and females, giving an appearance of three vertical bands. In life the procurrent caudal rays are green and the bases of the rays (above and below the median dark spot or spots) are orange. The anal fin is green in life, as are the pelvic fins. These fins are immaculate in preserved males, whereas females have occasional irregular flecks of brown on the rays. The pectoral fins are clear in both sexes and have brown spots on the rays which give the appearance of vertical bands, as in the caudal fin. Four or five bands are usually discernible, but are usually absent in breeding males.

The top of the head is dusky with four well developed ocular bars. The supraocular bar enters the eye and the preocular bars join across the snout. Small brown spots are scattered irregularly on the cheek and opercle. Similar spots are variably present or absent on the chin and branchiostegal membranes. The breast and belly are white and immaculate. A prepectoral dark brown spot is always present. In life, the cheek, opercle, and branchiostegal membrane are flushed with pale green.

The dorsum has seven blotches—one on the nape immediately anterior to the origin of the spinous dorsal fin, one on each side of the spinous dorsal and soft dorsal fins, and two on the caudal peduncle (The posterior blotch on the caudal peduncle is occasionally absent) (Fig. 3A and B). These blotches are dark brown in life and are usually separated from the dark vertical bars which extend down the side of the body to the anal fin base and encircle the caudal peduncle. In nonbreeding fish, the ground color of the body is tan, but breeding fish have bright green bars between the dark dorsal blotches and vertical bars. These green bars reach the belly but do not encircle it. In breeding males the center of each body scale has a small red spot. These spots appear as faint horizontal lines on the side of the body; they are occasionally visible as dark spots in preserved fish. No such spots are present in females. A dark humeral mark (on a projection of the supracleithrum or occasionally the postcleithrum) is present in both sexes.

Sexual dimorphism.—Sexual differences in color pattern have been discussed above. Breeding tubercles are present in males as whitened pads on the free edge of the midventral scales of the belly (anterior to the anal fin) and on the caudal peduncle. Tubercles are lacking on the pelvic and anal fins, although there are swollen ridges and tips on the rays of these fins. The tips of the lower pectoral rays are also slightly swollen. Tubercles were present in specimens collected as early as 23 March (CU 19662) and as late as 20 April (USNM 187578).

The genital papilla of the breeding female is a prominent, long tube which exceeds the length of the first anal spine and is slightly crenulate at its tip (Fig. 2). The male genital papilla is a small rodlike structure just inside the external opening of the cloaca. It is slightly enlarged in breeding specimens.

Geographic distribution and variation.—*E. thalassinum* is known from scattered locations throughout the Congaree and Wateree drainages, both above and below the fall line, which is not sharply defined in these rivers (Fig. 4). (Interestingly, the fall line acts as a sharp barrier to the distributions of *E.* (*Hololepis*) *saludae* (Hubbs and Cannon), *E.* (*H.*) *serriferum* (Hubbs and Cannon), and *E.* (*H.*) *fusiforme barratti* (Holbrook); Collette, 1962). To investigate geographic variation, the same kinds of meristic comparisons were made among the samples from several of the rivers as were made above among samples of the three species. The major rivers within the Santee system are the Wateree-Catawba and the Congaree, whose two main branches are the Saluda and Broad rivers. Only data on the lateral-line scale counts are presented here (Table 4); the detailed results of these comparisons are in Richards (1963). They show the greatest variation although the other meristic data show similar relationships. To test these variations, it was assumed that these distributions were approximately normally distributed. The means of the samples from the Congaree and the Wateree basins were compared ($t = 4.63$, $P <$ 000.1). The highly significant difference between samples indicates that the Congaree and Wateree populations are isolated from each other, even though the two drainages they occupy join to form the Santee. The large-river conditions at the juncture presumably act as a barrier to this riffle-dwelling species.

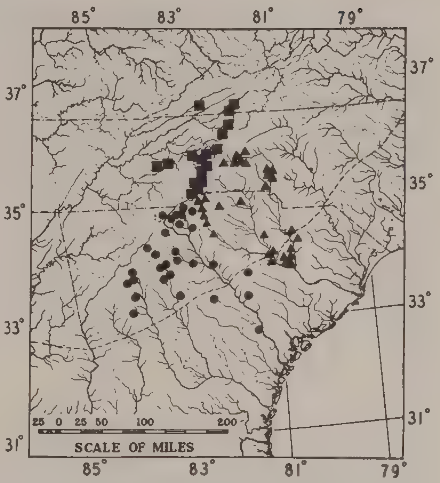

Fig. 4. Distribution of *Etheostoma thalassinum* (triangles), *E. inscriptum* (circles), and *E. swannanoa* (squares) in relation to the Fall Line (dashed line) in southeastern U. S.

Etheostoma inscriptum (Jordan and Brayton)
Turquoise darter

Nothonotus inscriptus Jordan and Brayton, 1878:34 (original description).

Etheostoma (*Rhothoeca*) *inscriptum*. Jordan, 1885:80 (listed).

Etheostoma (*Nanostoma*) *inscriptum*. Jordan and Evermann, 1896:1072 (description, range, partial synonymy).

Nanostoma inscriptum. Jordan, Evermann, and Clark, 1930:289 (partial synonymy). Jordan and Gilbert, 1882:512 (description).

Poecilichthys inscriptus. Schrenkeisen, 1938: 228 (characters, range).

Etheostoma inscriptum. Bailey and Gosline, 1955:16, 39 (subgeneric allocation, vertebrae). Moore, 1957:186, 191 (key, characters, range). Eddy, 1957:215 (listed). Richards, 1964:3899 (diss. abstr.).

Etheostoma thalassinus (*non* Jordan and Brayton, 1878:34). Boulenger, 1895:83 (in part; *Nanostoma inscriptum* incorrectly placed in synonymy).

Types.—Lectotype: USNM 31145 (female, 43 mm SL), Oconee River at Sulphur Springs, Hall Co., Ga.; summer 1877; D. S. Jordan and A. W. Brayton. Paralectotype: USNM 197439 (male, 42 mm SL). The paralectotype apparently was misplaced in another collection and was recently located by Dr. Collette. I have examined it and agree that it probably should be considered as a paralectotype (Collette and Knapp, 1966).

Diagnosis.—A species of the subgenus

TABLE 4. NUMBER OF LATERAL-LINE SCALES IN *Etheostoma thalassinum* FROM DIFFERENT AREAS IN THE SANTEE RIVER SYSTEM.

Drainage	38	39	40	41	42	43	44	45	46	47	48	49	50	n	$\bar{x}$
Congaree basin															
Saluda	–	1	5	11	18	9	7	13	5	–	1	–	–	70	42.91
Broad	–	2	4	7	8	7	8	4	–	2	–	–	1	43	42.74
Congaree	–	1	4	3	6	9	6	4	5	1	2	–	–	41	43.37
Total	–	4	13	21	32	25	21	21	10	3	3	–	1	154	42.99
Wateree basin															
Catawba	–	2	9	13	12	9	7	5	3	1	1	–	–	62	42.39
Wateree	2	6	16	19	17	1	4	1	–	1	–	–	–	67	41.10
Total	2	8	25	32	29	10	11	6	3	2	1	–	–	129	41.72
Grand total	2	12	38	53	61	35	32	27	13	5	4	–	1	283	42.41

Etheostoma with prevomerine teeth present, palatine teeth present or absent; dorsal blotches 6 (rarely 5); premaxillary frenum well developed; marginal red band in the spinous dorsal fin present; breeding tubercles present on ventral scales in breeding males; and branchiostegal membranes broadly connected. Head, cheek, opercle, prepectoral area, and breast naked; nape variably naked to fully scaled, with exposed or embedded ctenoid (rarely cycloid) scales; belly variably partly naked to fully scaled, with exposed ctenoid scales. Body coloration predominantly green; red present on head region; prominent red spots on body scales forming horizontal lines on males, particularly breeding males. Lateral-line scales (39) 44 to 52 (61). Vertebrae 38 or 39 (Bailey and Gosline, 1955: 16).

Coloration.—This description is based on preserved and living specimens. In color and pattern the fins agree with the description given above for *E. thalassinum.* The top of the head is dusky and has four ocular bars like those in *E. thalassinum.* The color of the cheek, chin, opercle, breast, and belly are like *E. thalassinum* except that breeding males have red on the opercle and cheek. A prepectoral spot is always present (see Figs. 1 and 2). The greatest difference between *E. inscriptum* and *E. thalassinum* is in body coloration. *E. inscriptum* has only six dorsal blotches (Fig. 3); it lacks the seventh blotch found on the procurrent caudal rays of *E. thalassinum.* Dark rectangular bars on the side of the body extend one to two scale rows below the lateral line. In life the body is a subdued green rather than tan, but the interspaces between the dark bars are bright green, as in *E. thalassinum.* The prominent red centers on each body scale in living males appear black and are prominent after preservation (Fig. 1).

Sexual dimorphism.—Sexual differences in coloration are given above. Breeding tubercles of breeding males are identical in shape and distribution to those of *E. thalassinum.* These tubercles were present in specimens collected as early as 25 March (CU 19548, CU 19755) and as late as 3 June (CU 37935). The genital papilla appears identical to that of *E. thalassinum* in both males and females (see Fig. 2).

Geographic distribution and variation.—Known localities of *E. inscriptum* are shown in Fig. 4. The meristic characters of specimens in samples from five areas (the Ocmulgee and Oconee rivers together form the Altamaha basin, the Savannah River above and below the fall line, and the Edisto River) were compared. The populations of these areas exhibit differences in dentition (Table 3) and scale counts, but little difference in fin-ray counts. These counts are given in detail by Richards (1963) and only lateral-line scale counts are shown here (Table 5). As would be expected, the greatest differences in these counts are among the major river systems (Altamaha, Savannah, and Edisto) rather than within any of these systems.

The Savannah and Altamaha samples are alike in scale counts, but differ sharply in palatine dentition (Table 3). The Edisto population is different from the Savannah and Altamaha populations in scale counts. In dentition, the Edisto sample is like that

TABLE 5. NUMBER OF LATERAL-LINE SCALES IN *Etheostoma inscriptum* FROM DIFFERENT AREAS IN THE ALTAMAHA AND SAVANNAH RIVER BASINS.

Drainage	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	n	x̄
Altamaha basin																									
Ocmulgee	–	–	–	–	1	–	2	2	4	4	4	5	1	1	2	–	–	–	–	–	–	–	–	26	48.46
Oconee	–	–	1	–	4	15	20	48	81	102	124	87	82	43	28	4	4	3	–	1	–	–	1	648	48.99
Total	–	–	1	–	5	15	22	50	85	106	128	92	83	44	30	4	4	3	–	1	–	–	1	674	48.95
Savannah basin																									
Above Fall Line	–	–	–	6	14	34	47	54	53	54	31	19	11	3	6	–	–	–	–	–	–	–	–	332	46.80
Below Fall Line	–	–	–	–	–	–	–	–	1	1	1	–	–	–	–	–	–	–	–	–	–	–	–	3	48.00
Total	–	–	–	6	14	34	47	54	54	55	32	19	11	3	6	–	–	–	–	–	–	–	–	335	46.81
Edisto basin	1	–	1	2	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	41.40
Grand total	1	–	2	8	20	49	69	104	139	161	160	111	94	47	36	4	4	3	–	1	–	–	1	1014	48.21

of the Altamaha. However, based on these data, the three populations (Altamaha, Savannah, and Edisto) do not warrant nomenclatural recognition.

Etheostoma swannanoa Jordan and Evermann
Swannanoa darter

Etheostoma swannanoa Jordan and Evermann, in Jordan, 1888:360 (original description). Boulenger, 1895:81 (description, synonymy). Bailey and Gosline, 1955: 16, 39 (subgeneric allocation, vertebrae). Moore, 1957:185, 191 (key, characters, range). Eddy, 1957:212, 214 (key, figure). Richards, 1964:3899 (diss. abstr.).

Etheostoma (*Nanostoma*) *swannanoa.* Jordan and Evermann, 1896:1070–1071 (partial synonymy).

Nanostoma swannanoa. Jordan, 1929:163 (description, range).

Poecilichthys swannanoa. Schrenkeisen, 1938: 228 (characters, range). Hubbs and Black, 1940:5 (characters). Bailey, 1948:79 (characters).

Types.—Lectotype: USNM 39861 (female, 60 mm SL), South Fork Holston River at Holstein (= Holston?) Mills, Va.; summer 1888; D. S. Jordan and B. W. Evermann. I hereby select this specimen from the two syntypes at the U. S. National Museum and designate it as the lectotype, because it has the same characters given in the original description, whereas the other specimen (USNM 125490) does not. Dr. Collette has kindly examined the syntypes in the other institutions; none agree so well with the original description as the lectotype (Collette and Knapp, 1966). Paralectotypes: USNM 125490 (female, 40 mm SL), South Fork Swannanoa River at Black Mountain, N. C.; Aug. 1888; D. S. Jordan, B. W. Evermann; original U. S. Bur. Fish. No. 772. SU 3507 (female, 41 mm SL), same locality as USNM 125490. SU 992 (2 males, 54–57 mm SL), the data given by Böhlke (1953:74) are the same as for USNM 39861, but Jordan and Evermann reported only two specimens from this locality; therefore SU 992 is probably from the Middle Fork of the Holston River at Marion (the other location listed in the original description).

Diagnosis.—A species of the subgenus *Etheostoma* with prevomerine teeth present, palatine teeth absent or rarely present; dorsal blotches 6; premaxillary frenum well developed; marginal red band in spinous dorsal fin present; breeding tubercles present on ventral scales in breeding males; and branchiostegal membranes broadly connected. Head, cheek, opercle, prepectoral area, and breast naked; nape usually fully scaled with exposed or embedded ctenoid (rarely cycloid) scales; belly fully scaled with exposed ctenoid scales. Body coloration predominantly brown particularly on the dorsum between blotches. Prominent red spots on body scales forming horizontal lines on males, particularly breeding males. Lateral-line scales (46) 48 to 58 (62). Vertebrae 40 to 43 (Bailey and Gosline, 1955:16).

Coloration.—This description is based on preserved and living specimens. The color pattern is similar to that of *E. inscriptum*, but differs in some features. In preserved specimens, the fin coloration of this species is similar to *E. thalassinum*, but in life the

TABLE 6. NUMBERS OF LATERAL-LINE SCALES IN *Etheostoma swannanoa* FROM DIFFERENT AREAS.

River Basins	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	n	x̄
Clinch	–	–	1	–	–	1	1	1	3	3	2	1	–	–	–	–	–	13	53.85
Holston	–	–	–	–	1	–	1	1	4	7	7	8	11	4	2	1	1	48	56.69
Watauga	–	–	–	–	–	–	–	1	–	1	2	3	–	2	1	–	–	10	56.90
Nolichucky	–	–	–	–	–	–	2	1	1	1	–	–	–	–	–	–	–	5	53.20
French Broad River counties: upstream to downstream																			
Transylvania	1	4	5	2	3	6	4	2	1	–	–	–	–	–	–	–	–	28	49.86
Henderson	–	–	4	3	1	5	7	4	–	2	–	–	–	–	–	–	–	25	51.12
Buncombe	–	–	2	4	9	10	8	13	7	5	2	2	1	–	–	–	–	63	52.29
Madison	–	–	–	–	4	1	7	4	7	3	3	4	–	–	1	–	1	35	53.94
Cocke	–	–	1	–	1	–	3	1	5	2	1	3	4	1	1	–	–	23	55.00
Sevier	–	–	1	–	2	2	2	4	4	4	3	2	1	3	1	–	–	29	54.45
French Broad Total	1	4	13	9	20	24	31	28	24	16	9	11	6	4	3	–	1	204	52.71
Grand total	1	4	14	9	21	25	35	32	32	28	20	23	17	10	6	1	2	280	53.60

spinous dorsal fin of the male *E. swannanoa* has two orange bands—one submarginal and the other along the base of the fin. This basal band is similar to that in the *blennioides* group. In males, equal concentrations of micromelanophores are present on the interspinous membranes of the entire spinous dorsal—not on just the first and last few interspinous membranes as in the other two species. The pectoral fins are green, but in breeding fish of both sexes they are bright orange at the base and lower edge.

The head has four well developed ocular bars and in life is pale green, with a light brown bar above the posterior ocular and preocular bars. The ground color of the dorsal surface of the body is pale green in breeding males and slightly darker green in breeding females. The ventral surfaces are pale green in breeding males and white in breeding females. Nonbreeding specimens have a tan or pale green color dorsally and ventrally. Six dark dorsal blotches are present in the same location as those of *E. inscriptum*. The second, fourth, and sixth blotches are often reduced or absent in specimens in breeding condition. The dark bars on the side are similar to those of *E. inscriptum* but are greatly reduced in breeding specimens (Figs. 1 and 2). The center of each body scale has a red spot; these spots form horizontal red lines on living specimens and dark lines on preserved specimens. One striking feature of living specimens is an area of deep rich brown on the nape between the head and first dorsal blotch.

Sexual dimorphism.—Sexual color differences are described above. Breeding tubercles and swelling of fins are like those in *E. thalassinum* and *E. inscriptum*. These tubercles and swellings are found only in males and were present on specimens collected as early as 23 March (VPI uncat.) and as late as 8 June (CU 37963).

The genital papillae of the breeding males and females are similar to those of *E. thalassinum* and *E. inscriptum*, except that in the females they are much larger and more prominent (Fig. 2C).

Geographic distribution and variation.—The localities at which this species has been collected are shown in Fig. 4. The species is now present sporadically in Tennessee headwaters; only small samples were obtained from the Clinch, Holston, Watauga, and Nolichucky rivers. Mine pollution and impoundments have eliminated most of the suitable habitats and account for the small samples. A comparison of the meristic characters among these rivers reveals only slight differences (Richards, 1963). Material from the French Broad River was adequate, however, for a comparison of lateral-line scales by counties (Table 6), and a clinal variation was revealed. (Counties were used rather than elevations because these geographic boundaries conveniently separate upstream and downstream portions of this river.) The fishes in headwater populations have large scales (Transylvania County), whereas those downstream have slightly finer scales (Sevier and Cocke counties). Elevation may account for this variation, since the French Broad River is at approximately 2000 ft in Transylvania County and approximately 1000 ft in Sevier and Cocke counties.

MATERIAL EXAMINED

Etheostoma thalassinum. All material is from the Santee river system.
Catawba River: 72 specimens: (26–57 mm SL). CU 10058, 10113, 10120, 10906, 11260, 11673, 19292, 19298, 19336, 19407, 19544; UMMZ 138493, 138494; USNM 40530, 92546, 92548, 187575, 187591, 187592; ANSP 70745–6; CM 62.1.884, 62.1.885.
Wateree River: 67 specimens (25–65). USNM 187567, 187569, 187570, 187574, 187580, 187581, 187589, 187590, 187594, 187595.
Broad River basin: 47 specimens (30–56). CU 9802, 9806, 19213, 19662, 19683, 19697; USNM 40609, 162945.
Saluda River: 71 specimens (27–63). CU 10920, 10924, 37871, 37973; USNM 162353, 187568, 187571, 187572, 187573, 187577, 187582, 187583, 187588; SU 987.
Congaree River: 41 specimens (40–62). CU 25863; USNM 34004, 187576, 187579, 187584, 187585, 187586, 187593.
Etheostoma inscriptum.
Altamaha River: 674 specimens (24–66). CU 10932, 17426, 17508, 17521, 18193, 19812, 29729, 29733, 29742, 43582; UMMZ 88305, 158011; USNM 165727, 165732, 165734; ANSP 79452; UG 4, 68, 104, 106.
Savannah River: 395 specimens (29–63). CU 10927, 17367, 17451, 19070, 19548, 19738, 19755, 19783, 19818, 29740, 29743, 37913, 37935, 38136, 42884; UMMZ 156103, 165546; USNM 162520, 168095, 168112; UG 22A, 22C, 60, 163, 313, 369, 389, 501, 509.
Edisto River: 6 specimens (34–46). CU 15134, 15139.
Etheostoma swannanoa. All material is from the headwaters of the Tennessee River.
Clinch River: 15 specimens (40–71). VPI 1055; UMMZ 129048, 129076, 171338.
Holston River: 62 specimens (32–75). CU 9945, 19181, 20951, 21511, 37629, 37630, 37900, 41842; UMMZ 138521; VPI 608; SU 3507.
Watauga River: 11 specimens (33–68) . UMMZ 157423, 157468.
Nolichucky River: 7 specimens (45–53). CU 29243, 44178; ANSP 66170–1.
French Broad River: 353 specimens (21–67). CU 9979, 9998, 13851, 18579, 18580, 18581, 21501, 22259, 22262, 22866, 22880, 22901, 22920, 22928, 22939, 22950, 25177, 29257, 29297, 29425, 29461, 29549, 37631, 37632, 37715, 37886, 37963; UMMZ 109502, 129254, 131410, 131424, 131498, 132775, 155905, 155919, 155928, 155934, 155945, 155967, 155980, 155992, 156005, 156026, 156041, 156053, 156073, 156081, 156092, 156121, 156149, 156162, 156196, 156218; VPI uncat., 1410, 1420, 1623; USNM 40502, 164162, 164163, 190877; SU 3507.

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18

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The immune response in teleosts

THE CAPABILITY OF TELEOSTS to respond to antigenic stimulation with specific immune responses (adaptive immunity) has been known since the early part of this century. Most of the early studies of the immune response in teleosts were made by persons interested in the pathology of cultured fishes. Thus the capacity of teleost fishes to produce specific bacterial agglutinins and to develop protective immunity had been studied reasonably well before 1950. Many of these early studies noted that the immune response of teleost fishes as well as that of other poikilothermic vertebrates was markedly influenced by the environmental temperature.

More recently the immune response of teleost fishes has received additional study because of interest in the immunogenetics of these animals and because of the recognition of the importance of comparative immunologic studies to better understanding the immune response and its evolutionary development (14, 21, 24).

In this report we shall briefly review the varieties of immune responses that have been demonstrated in teleost fishes and the influence of temperature upon them. These include the production of agglutinating and precipitating antibodies, anaphylaxis, tissue transplantation immunity, delayed hypersensitivity, and anti-viral antibodies. We shall also discuss evidence from our own and other laboratories on the organ and cellular site of antibody production in teleosts and on the properties of the teleost proteins which possess the attributes of immune globulins.

PRODUCTION OF AGGLUTININS BY TELEOSTS

The production of antibacterial agglutinins is perhaps the most studied immune response in teleost fishes. Babes and Riegler (2) demonstrated the production of agglutinins for *Proteus piscidus versicolor* by cruscians (*Carrasius vulgaris*) and tench (*Tinca vulgaris*). Bergman (5) and Aaser (1) each demonstrated the production of agglutinins for *Vibrio anguilla* in northern pike (*Esox lucius*).

Nybelin (44) held eels (*Anguilla anguilla*) at 8°C and at 18°C and injected them with strains of *Vibrio*. Those held at 18° C produced detectable agglutinins while those held at 8° C did not.

Strain-specific agglutinins for *Pseudomonas punctata* were shown to be produced in carp (*Cyprinus carpio*) by Snieszko and his co-workers (61, 63) and by Pliszka (49, 50). They also noted the influence of the environmental temperature, obtaining higher titers at 18-20° C than at 12-12.5° C. In experiments reported by Smith (60), agglutinins for *Bacterium salmonicida* were produced in carp, rainbow trout (*Salmo gairdneri*), and brown trout (*S. trutta*) after intraperitoneal injections of a heat-killed vaccine. These experiments were unique in that they were carried out at 10°C, a lower temperature than antibody production in cold-blooded animals had been demonstrated previously.

Cushing (13) further demonstrated the effect of temperature on antibody production in fish. Goldfish (*Carassius auratus*) and carp were injected intraperitoneally with suspensions of sea urchin (*Strongylocentratus purpuratus*) sperm. A rise in agglutinin titer occurred 11 days after injection in fish held at 28°C, while the titer did not rise until 15 days after injection in the fish held at 14°C.

The effect of environmental temperature on antibody production in both frogs and fish was investigated by Bisset (8, 9) with the conclusion that the release of the antibody, rather than its formation, is inhibited at lower temperatures. Animals immunized at low temperatures released significant amounts of antibody when injected with adrenal cortical extract. This phenomenon should be studied further in fishes.

Barrow (3) found that both temperature and social behavior influenced the ability of tench, perch (*Perca fluviatilis*), and goldfish to produce lytic and agglutinating antibodies for trypanosomes. Fish held at 10°C did not eliminate infecting trypanosomes. When the fish were moved to 20°C they eliminated the trypanosomes and produced lytic and agglutinating antibodies. This response was influenced by the position the individual fish held in the aquarium "peck order" with only those high in the "peck order" responding.

Many of the studies on the effect of temperature on antibody formation in poikilothermic vertebrates indicated that no response occurred below about 10°C. This prompted us to consider the immune response in fishes which spend most of their life at temperatures below 10°C. Since they live and grow, they must possess some compensatory mechanism allowing protein synthesis at these lower temperatures. Thus antibody production should also be possible. The immune response of the sablefish (*Anaplopoma fimbria*), a fish which lives in the cold waters of the North Pacific, was investigated (52). Detectable agglutinins were produced at 5°-8° C in as little as 27 days by seven injections of foreign erythrocytes. Titers increased over periods of five months at 6°-9 °C, reaching 1:8000 in one case.

In our group (36) some studies have also been made on the production of agglutinins in rainbow trout held at 15° C for chicken erythrocytes and for heat-killed cells of an unidentified bacterium, an etiologic agent of "red mouth" disease in rainbow trout. Three injections were given at three-week intervals and bleeding taken 3-12 days after the last injections. In the case of those trout injected with chicken erythrocytes, only one of 20 fish had saline agglutinins detectable at 1:4 dilution, but nine of the 20 had antibodies detectable at 1:4 with a Coombs-type anti-rainbow-trout globulin. In the case of those trout injected with heat-killed bacteria, 12 of 20 fish had saline agglutinins detectable at both 1:4 and 1:8. All 20 had antibodies detectable with the antiglobulin test. In a control group, two out of 20 fish had saline agglutinins and four others had antibodies detectable with the antiglobulin serum. This points up the importance of testing for incomplete antibodies in studies of the immune response.

Post (51) has made an extensive study of the immune response of rainbow trout to *Aeromonas hydrophila.* He sampled the immune response in five groups of 100 fish held at 15.6° C. The five methods of administration of the bacteria were: intramuscularly in either saline or in Freund's complete adjuvant, intraperitoneally in either saline or in Freund's adjuvant, or orally. There was no significant difference between the two parenteral routes of administration. Detectable antibody was produced in most fish after two injections of saline-suspended bacteria at a 27-day interval and 28-32 days after a single injection of adjuvant-suspended bacteria. The rate of antibody synthesis was slower in the adjuvant-treated group but remained at a higher titer longer. The highest titer reached was 1:64. Fish with titers of 1:4 or greater were found to be resistant to challenge with one LD_{90} dose of living bacteria. Continuous oral immunization with heat-killed bacteria produced measurable but low agglutinin production in all fish sampled after 192 days. Other investigators (18, 40, 57, 62, 65) have studied the response of several salmonid species to oral immunization with killed bacterial pathogens. In some cases, evidence has been obtained for the production of significant levels of protective antibodies.

Krantz, Reddecliff, and Heist (39) studied the immune response of brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) held at 11° C to *Aeromonas salmonicida,* the cause of a serious disease known as furunculosis. Single injections of formalin-killed bacteria were made in saline suspension or incorporated in an incomplete Freund's adjuvant. Maximum agglutinin titers were obtained three months after the injection. Mean peak titers of up to 1:160 were obtained with injection of the saline suspension, but these dropped off rapidly. Injection of the adjuvant vaccine resulted in mean peak titers as high as 1:5166. High titers and protective immunity to challenge injection with an LD_{50} of viable bacteria persisted for as long as 24 months in brown trout injected with adjuvant vaccine.

Clem and Sigel (10) immunized margates (*Haemulon albium*) with weekly intraperitoneal injections of heat-killed *Salmonella paratyphi* B for three to six weeks. Agglutinin titers of pooled sera from fish receiving five injections were as high as 1:160.

Spence *et al.* (65) demonstrated the production of agglutinating antibodies for *A. salmonicida* in rainbow trout held at an average temperature of 12° C and given multiple injections of formalin-killed bacteria over a period of several weeks. Titers as high as 1:5120 were obtained. The sera from the immunized trout were shown to passively immunize juvenile coho salmon (*Oncorhynchus kisutch*). Oral immunization was ineffective.

The production of immune isohemagglutinins in goldfish was studied by Hildemann (27, 29). Saline agglutinin titers ranging from 1:4 to 1:2048 were produced after nine injections given over a period of three weeks. Apparently all fish responded with detectable isoagglutinins.

We have reported (52, 54) results of some isoimmunizations of rainbow trout and sockeye salmon (*Oncorhynchus nerka*). Isoimmunization of 140 sockeye salmon held at temperatures from 9° to 14° C and injected over periods of two to three months with whole blood resulted in the production of saline isoagglutinins with titers ranging from 1:2 to 1:8 in 15 fish. Forty of the recipients were adults returning from the sea to spawn. None of them produced detectable antibodies. The immune mechanism of these fish is possibly abnormal as are many other physiological mechanisms in spawning salmon.

In our early studies on trout, 156 individuals were isoimmunized with whole blood. Only about half of them survived a full course of nine injections. Of the survivors, 27 produced detectable isoagglutinins with titers ranging from 1:2 to 1:64. All of these fish were held in spring water of constant 15° C temperature. Some of the sera had markedly higher titers when diluted with normal serum than when diluted with saline, indicating the presence of incomplete antibodies. In one of our more recent studies, 96 rainbow trout held at 15° C were isoimmunized; of these, 60 produced detectable hemagglutinins with titers varying from 1:2 to 1:256. Sanders and Wright (58) have also successfully produced isohemagglutinins in rainbow trout. Bingham (7) has produced isoagglutinins in cutthroat trout (*Salmo clarki*) by a single injection of alum precipitated muscle tissue.

PRECIPITIN PRODUCTION IN TELEOST FISHES

The ability of teleost fishes to produce precipitating antibodies has only recently been reported. Post (51) found precipitins in the serums of rainbow trout immunized with *Aeromonas hydrophila* for crude protein extracted from the bacteria. Ross and Klontz (56) have also produced precipitating antibodies in rainbow trout for soluble bacterial antigens. Clem and Sigel (10) demonstrated the production of weak precipitins for bovine serum albumin (BSA) by margates. Margates were injected intraperitoneally with 4.5 mgm of BSA in saline at weekly intervals for three to six weeks. Pools of serum obtained over a period of three to eight weeks were tested by the Ouchterlony immunodiffusion method. Eighteen of 24 pools from immunized fish precipitated, while five pools from normal fish did not.

A hemagglutination titer of 1:50,000 was obtained when tanned sheep cells coated with BSA were tested with pooled immune margate sera. One of us (H.O.H.) has started an investigation of the response of rainbow trout to soluble antigens. Precipitins detectable by Ouchterlony immunodiffusion methods have been produced in trout injected with BSA in saline or in Freund's adjuvant. Production of precipitins for hemocyanin in a teleost fish, the black bass (*Micropterus salmoides*), and in the holostean fish *Amia calva* has been reported by Papermaster *et al.* (45).

The Immune Response in Teleosts to Viruses and Bacteriophages

Only in recent years has the immune response in teleost fishes to viruses and bacteriophage been studied. Uhr *et al.* (67) investigated the immune response of five goldfish held at 30° C to injections of 10^{10} phage ΦX174 particles. The production of neutralizing antibodies in two to four weeks was demonstrated. Some characteristics of the goldfish antibodies studied by Uhr and his co-workers will be discussed in a later section.

Papermaster *et al.* (47) have investigated the response of the bullhead (*Ameiurus melas*) to T_2 phage at 10° C. The injected phage particles were cleared from the circulation in four days, the circulating neutralizing antibodies were detected in a blood sample taken on the fourteenth day.

Clem and Sigel (10) injected margates intraperitoneally with influenza virus suspension at weekly intervals for three or more weeks. Antibodies were detected by the hemagglutination inhibition (HI) test in titers up to 1:640. Uninjected controls had HI titers as high as 1:40. Later studies reported by Sigel and Clem (59) indicate that there is a deficiency in the anamnestic response in fishes immunized with viruses.

Klontz *et al.* (38) have studied the immunopathological aspects of several virus diseases of *Salmonidae*. Only a suggestion of neutralizing antibody activity and no precipitating antibody was detected. An increase in lymphocytopoietic activity in the anterior kidney was noted four to five days after virus injection.

Anaphylaxis in Teleosts

The only report of successful production of anaphylaxis in teleosts known to the authors is that of Dreyer and King (16). Fifty individuals of four fresh-water species (fresh-water perch, common sunfish, rock bass, and goldfish) were injected intraperitoneally with a sensitizing dose of 0.2 ml of horse serum. After 15 days a shocking dose of 0.1 ml horse serum was injected intraperitoneally. Shocked fish showed symptoms of uneasiness, curling of the fins, and an increase in excursions of the gill clefts. No fatalities occurred. Specificity of the reaction was demonstrated in control tests with egg albumin; fish sensitive for horse serum did not react when injected with egg albumin but were later found to have developed sensitivity to egg albumin as a result of the test injection.

Delayed Hypersensitivity in Teleosts

There are few details in the literature on the delayed hypersensitivity reaction in teleost fishes. The inflammatory response noted in the teleost homograft reaction, which will be discussed in a later section, may possibly be an example of delayed hypersensitivity. The relationship of the homograft reaction to delayed-type hypersensitivity has been reviewed by Lawrence (42) and by Billingham and Silvers (6). However, the extent of this relationship has not been clearly established in mammals and can only be hypothesized in fishes. An inflammatory response to intramuscular injection of complete Freund's adjuvant has been reported in bullheads (*Ameiurus melas*) by Papermaster *et al.* (47) and in trout by Post (51). Papermaster *et al.* (46) have reported that the bullhead shows delayed sensitivity following tuberculin sensitization.

One of us (H.O.H.) has demonstrated a positive delayed corneal reaction to PPD in rainbow trout one month after they were immunized with complete Freund's adjuvant. The reaction reached a peak in 3-5 days and lasted 12 days. These fish also had a granulomatous reaction at the site of the intraperitoneal injection of the complete adjuvant. Unimmunized control fish injected intracorneally with PPD showed only a transient faint clouding which disappeared after two days. More extensive studies of delayed hypersensitivity in teleosts are certainly warranted, especially in light of the important role delayed hypersensitivity plays in certain theories of the mechanism of antibody production (48).

HOMOGRAFT IMMUNITY IN TELEOSTS

The subject of the immune response to homografts in teleost fishes has been actively studied by several groups of investigators in recent years (12, 25, 28, 29, 30, 31, 33, 34, 35, 66). Goldfish, surfperch (*Cymatogaster aggregata*), platyfish (*Xiphophorus maculatus*), killifish (*Fundulus heteroclitus*), and other fishes have been found to reject homografts, further establishing the immunological competence of teleosts. Hildemann (28, 29) has shown that the rejection of foreign scale grafts is an inflammatory response which is temperature-dependent, the median survival times of grafts being shorter at higher temperatures. Accelerated rejection of second-set grafts established anamnesis and the immunologic nature of the response. The homograft reaction in teleosts has been profitably used to study a number of basic problems in genetics, population biology, immunologic tolerance, and the effect of x-rays and antimetabolites on antibody synthesis. It promises to be a fertile field for further research on comparative and developmental immunology. For a more detailed treatment, the reader is referred to the excellent review by Hildemann and Cooper (30).

THE ORGAN AND CELLULAR SITES OF THE IMMUNE RESPONSE IN TELEOST FISHES

The existence in teleosts of most of the tissues and cells currently known to be associated with the immune response has been recognized for a long time. These include lymphoid tissue, the thymus, lymphocytes, and plasma cells. This subject has recently been extensively discussed and reviewed (24, 38, 46) and will not be considered in detail here.

The demonstration through independent methods by Fagraeus (20), Good (23), Coons *et al.* (11), and others of the importance of the plasma cell in antibody formation led to a study in our group on the organ and cellular site of antibody production in rainbow trout (36). This study was patterned somewhat after that of Makinodan *et al.* (43) on chickens. Trout were stimulated with chicken erythrocytes or killed bacteria, and the cytology, histology, and serology were studied and correlated. Unfortunately, statistically significant correlations could not be established because of the low magnitude of the immune response and of cellular proliferation. These studies have been repeated and extended and are the subject of a report presently in preparation (37).

The virtual absence of both plasma cells and γ-globulin in some teleosts has been noted by two groups of investigators (4, 19), with the conclusion that plasma cells are probably involved in γ-globulin synthesis.

Obviously, the direct demonstration of a relationship between the proliferation of given cell types and immune responses in teleosts is fertile field for research in comparative immunology. The teleost thymus, excellently described by Hafter (26), would seem to be an especially good subject for experimental manipulation and study in connection with its role in the ontogeny of the immune response.

THE PHYSICOCHEMICAL CHARACTERISTICS OF TELEOST ANTIBODIES

Extensive studies on antibodies of higher animals, especially those on germ-free animals, reviewed in (24), lead to the conclusion that all or nearly all of the γ-globulin in the serums of mammals and birds is antibody. Additional components of normal mammalian serums with the properties of immuno-globulins have the electrophoretic mobility of slow β-globulins. These are related but not identical to γ-globulin in their antigenic structure. Moving boundary, paper, and starch-gel electrophoretic studies on the normal sera of teleost fishes have indicated a very low content of protein with the mobility of mammalian γ-2 globulin (4, 15, 17, 19, 51). However, Fine and Drilhon (22) have found by immunoelectrophoresis an increase in eel (*Anguilla anguilla*) serum of a component with the mobility of γ-2 globulin on repeated injection of the fish with human serum, and Uhr *et al.* (67) found that the antibodies produced in goldfish after immunization with phage ΦX174 had electrophoretic mobilities corresponding to human γ-1 and γ-2 globulin.

The majority of the antibody activity was in the γ-2 fraction after only 2-4 weeks immunization and the proportion in this fraction increased with increased time of immunization. These authors also found that the goldfish antibody activity was evenly distributed between slowly- and rapidly-sedimenting fractions after two months, but after five months it was almost entirely in the slowly-sedimenting fraction. Unlike the antibodies of higher animals, the antibody activity of serums taken both early and late in the immunization were sensitive to treatment with 2-mercaptoethanol.

Papermaster *et al.* (45) have demonstrated by immunoelectrophoresis a component with electrophoretic mobility similar to human γ-globulin in the holostean fish *Amia calva*.

Sorvachev *et al.* (64) have reported that hyperimmunized carp have increased amounts of γ-globulin and that this increase is passed on to their progeny.

Clem and Sigel (10) have shown that the precipitating antibodies produced in margates for BSA have the mobility of fast γ-globulins.

Post (51) found that the agglutinating antibodies in a large serum pool from rainbow trout immunized with killed *Aeromonas hydrophila* were precipitated by 20% sodium sulfate and had the electrophoretic mobility on paper of β-globulins.

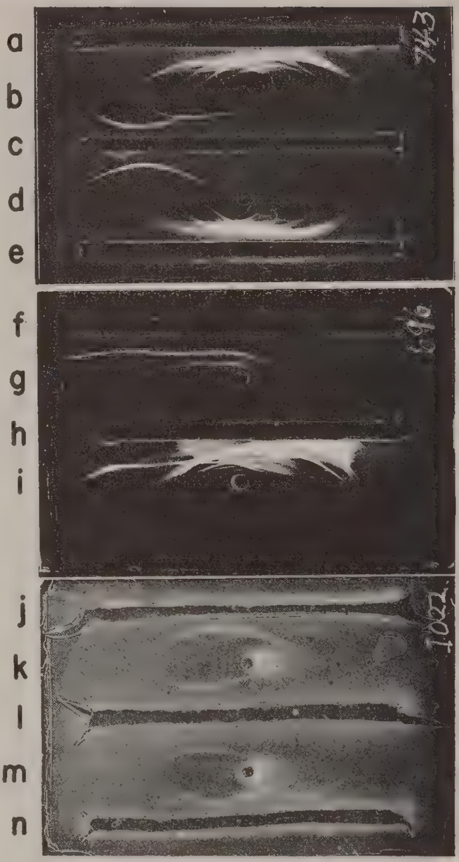

FIG. 1. Immunoelectrophoretic comparison of sockeye salmon serums, rainbow trout serums, and human serum. (a and e: anti-sockeye salmon serum. b, d, and g: sockeye salmon normal serum. c and f: anti-sockeye salmon hemolysate. h: anti-human serum. i: normal human serum. j and n: anti-rainbow trout serum. l: anti-rainbow trout immunoglobulin. k and m: normal rainbow trout serums.)

We have made extensive studies of the serum proteins of salmonid fishes by immunochemical and electrophoretic methods (32, 41, 55). Both paper and starch-gel electrophoretic observations have confirmed that the serums of salmon and rainbow trout have so little γ-2 globulin that it is virtually undetectable. Most antisera prepared in rabbits by immunizing with sera of salmon or trout do not detect appreciable quantities of γ-globulin on immunoelectrophoresis. We have, however, produced potent anti-globulin sera by two methods. One is by immunizing rabbits with hemolysates of washed sockeye salmon (*Oncorhynchus nerka*) erythrocytes incorporated into Freund's adjuvant. Several components are detected by these sera (Fig. 1). One β-globulin component is probably a haptoglobin since it complexes with hemoglobin. Other components, including one with γ-2 mobility in some fish, are probably immunoglobulins.

The other method used to produce potent precipitating sera was designed to detect immunoglobulins specifically. Either naturally-occurring hemolytic and agglutinative antibodies for rabbit erythrocytes, which occur in the sera of rainbow trout and chinook salmon (*Oncorhynchus tshawytscha*), or immune antibodies for rabbit or chicken erythrocytes produced in rainbow trout were adsorbed onto the cells of rabbits or chickens; the cells were then washed exhaustively and injected into the rabbit or chicken. Antisera produced in this way detect a single component in most sera with γ-1 (β-2) mobility (32). The one produced with chinook salmon antibodies cross-reacts completely with one of the components in the anti-hemolysate sera. Our studies, some of which will be reported in more detail elsewhere (32, 68), indicate that the immunoglobulins of salmonid fish are quite heterogeneous, both antigenically and electrophoretically. The immunoglobulin found in most sera has the mobility of a γ-1 globulin, but some sera contain detectable amounts of γ-2 globulin. Some examples are presented in Fig. 1.

The association of immunoglobulins with hemolysates is unusual and could possibly be due to contamination of the preparations with white cells. However, care was taken to remove the buffy coat from these preparations. More convincing evidence that the immunoglobulins are adsorbed to the surface of the erythrocytes is provided by the observations that specific anti-immunoglobulin sera agglutinate salmonid red cells, and that the activity of the anti-immunoglobulin sera can be removed by absorption with washed normal salmon erythrocytes. The significance of these observations is under investigation.

CONCLUSION

It is evident from the foregoing treatment that the teleosts are at a relatively advanced stage in the evolutionary development of the immune response. Most of the immune responses known in mammals and birds also exist in teleosts. There is some evidence for deficiencies of a quantitative rather than a qualitative nature. However, these are possibly due in part to the lower body temperature. Some of the quantitative deficiencies are probably characteristic of the species investigated. Immunologists recognize that some mammals are good precipitin producers, others are not; and extreme cases exist like the agammaglobulinemic humans who produce no humoral antibodies. Therefore, we should not consider a few goldfish or trout as representative of all the teleosts.

This highly variable group of animals seems to the authors to abound with possibilities for research, both on the macroevolutionary aspects of comparative immunology, and on the genetic, microevolutionary aspects.

Perhaps in the poor fish there will be found some of the answers to the most profound questions of biology and medicine.

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The Location of the Termination Area of the Equatorial Undercurrent in the Gulf of Guinea Based on Observations during Equalant III[1]

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During the Equalant III program in the spring of 1964, the Equatorial Undercurrent in the eastern part of the Atlantic Ocean was followed into the inner part of the Gulf of Guinea. The high-salinity core associated with this current maintained salinities of more than 36.2‰ as far east as the Island of São Tomé. Near 6½°E the subsurface salinity maximum turned to a southeasterly direction, its maximum salinity gradually decreasing in the core. Salinities in excess of 36.2‰ could be observed as close as 150 km off the coast of Africa near 1°20′S. Current-drogue measurements in and around the high-salinity core indicate that in April 1964 the undercurrent terminated very close to the Island of São Tomé.

As part of the Equalant III program, from February through April 1964, the R.V. *Pillsbury* of the Institute of Marine Science, University of Miami, and the R.V. *Geronimo* of the Bureau of Commercial Fisheries cooperated in an oceanographic current survey of the inner part of the Gulf of Guinea. Of particular interest was the investigation of the eastern extension of the Equatorial Undercurrent. Only those data which were obtained between 2°N and 2°S and which pertain to this particular problem will be considered in this report.

The Equatorial Undercurrent in the Atlantic Ocean has been explored in great detail during the past few years. Most of our present knowledge about this important branch of the equatorial current system in the Atlantic Ocean has been contributed by expeditions under the programs of the International Cooperative Investigations of the Tropical Atlantic (ICITA).

An outstanding feature of the Atlantic Equatorial Undercurrent is the subsurface core of high-salinity water which is probably associated with the main current axis. The question whether the maximum salinity coincides with the maximum speed of the current is not yet answered. However, during previous equatorial expeditions it was shown by direct current measurements that the high-salinity core is an essential feature of the undercurent and can be used as an indicator of this current. [*Metcalf et al.*, 1962; *Neumann and Williams*, 1965].

During the period between March 5 and April 1, 1965, R.V. *Pillsbury* and R.V. *Geronimo* completed oceanographic sections along the meridians 15°W, 8°W, 4°W, 2°W, and 0° longitude. A leap-frog technique was used by which the *Pillsbury* adjusted the position of her sections on the basis of results obtained by *Geronimo* working farther to the east.

A typical salinity section, Figure 1, is based on observations by R.V. *Pillsbury* along 8°W.

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[1] Contribution 694, Institute of Marine Science, University of Miami. Contribution 40, Geophysical Sciences Laboratory, Department of Meteorology and Oceanography, New York University. Contribution 29, Bureau of Commercial Fisheries, Tropical Atlantic Biological Laboratories, Miami, Florida.

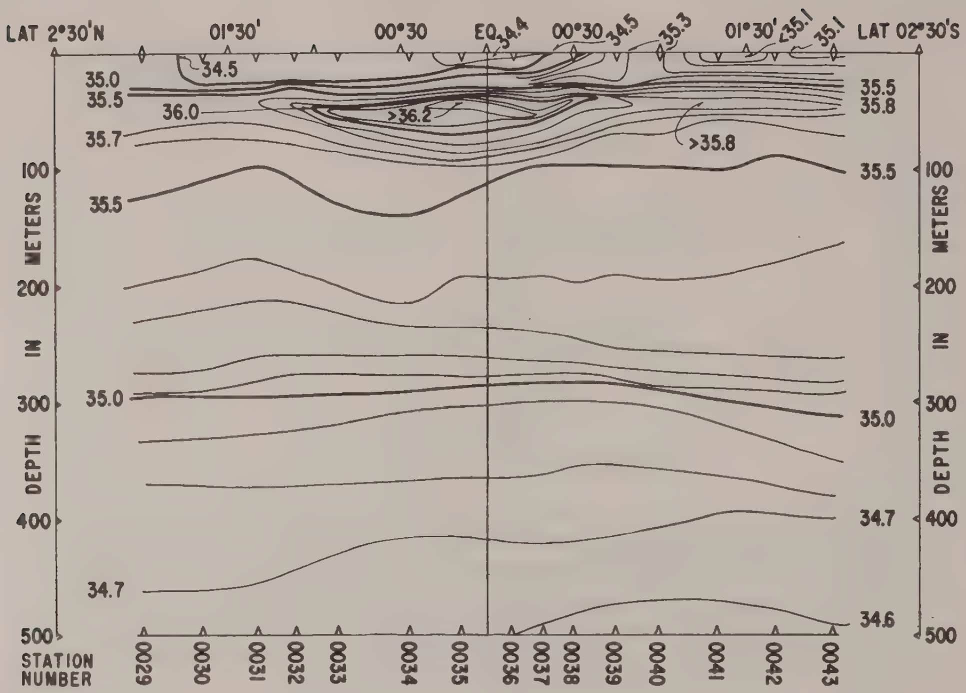

Fig. 1. Salinity section between 2°N and 2°S along 8°W, March 17–19, 1964. Stations numbers are given along the bottom line of the section. Salinity in parts per thousand.

A similar section along 8°W was completed by *Geronimo* on March 11 and 12. As shown in Figure 1, the maximum salinity in the core was above 36.2‰ at a depth of approximately 45 to 50 meters at the equator. After each *Pillsbury* section, drogue measurements were made at the depth of the salinity maximum at selected points across the salinity core. The drogues used by *Pillsbury* were equipped with time-depth recorders which were recovered to confirm that the drogues were drifting at the depth of the salinity maximum. During *Geronimo* sections, parachute-drogue measurements were made at or near the equator at the depth of the salinity maximum.

After completion of the planned survey west of 0° longitude, it was necessary for *Geronimo* to terminate her cooperation in this program because of other commitments. Examination of the data obtained up to this time indicated that the Equatorial Undercurrent extended farther eastward than had originally been anticipated. Because of time limitations for *Pillsbury,* it was therefore decided to alter the survey program in such a way that the *Pillsbury* would terminate her meridional oceanographic sections and proceed eastward along the equator, occupying oceanographic stations every 110 km and making drogue measurements every 220 km until the end of the undercurrent was reached. At the conclusion of this survey a closely spaced network of meridional oceanographic sections with drogue measurements was planned in the vicinity of the termination point of the undercurrent.

Results of the observations taken during this survey are shown in Figures 2 through 9. On the basis of oceanographic station data obtained along the equator, a zonal salinity section (Figure 2) shows a well-defined, high-salinity core of more than 36.2‰ extending from nearly 13°W to 6½°E. This core occupies a relatively thin layer of water at depths around 50 meters and disappears in the zonal section along the equator near 6°E. As will be demonstrated later, this core trends southeastward until it gradu-

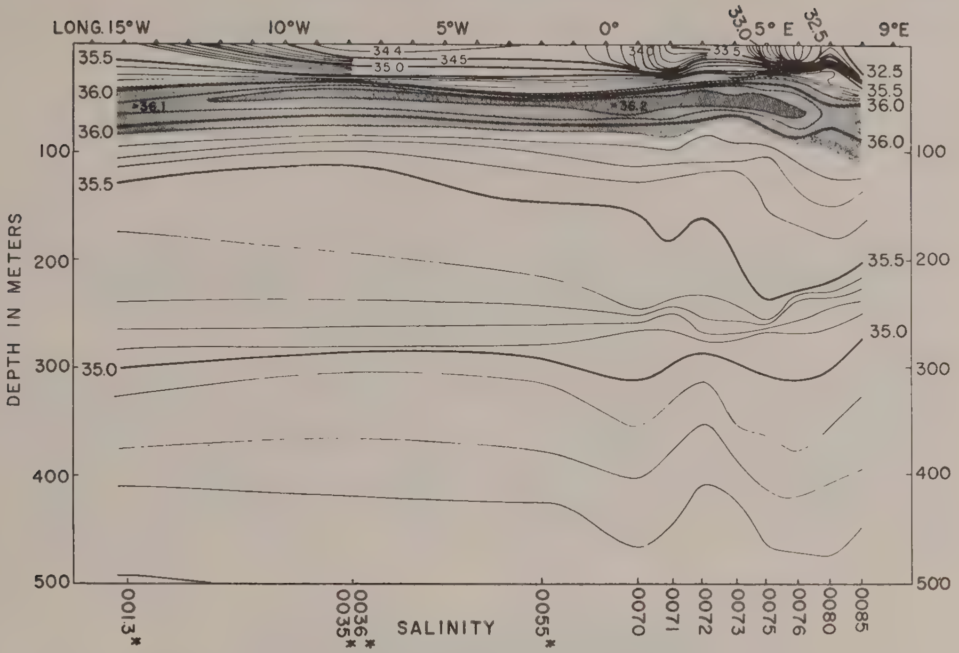

Fig. 2. Salinity section between 15°W and 8°E along the equator, March 10 to April 6, 1964. Station numbers are given along bottom line of the section. Asterisks indicate data taken from vertical salinity sections along 15, 8, and 2°W.

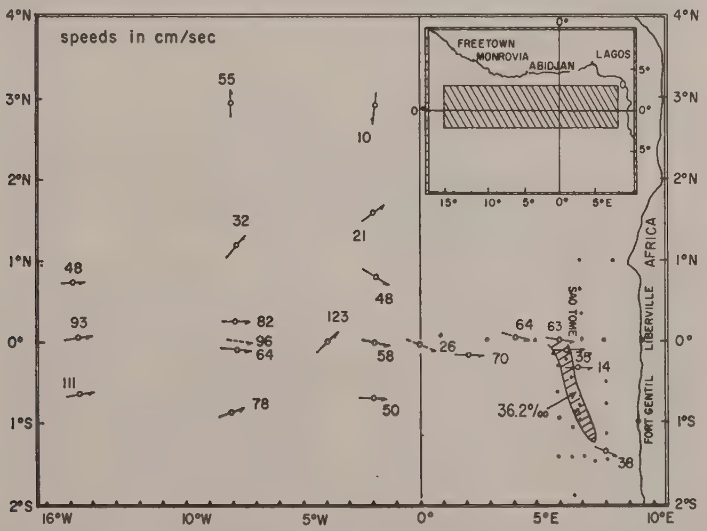
speeds in cm/sec
4°N
3°N
2°N
1°N
0°
1°S
2°S
16°W
10°W
5°W
0°
5°E
10°E
55
10
32
21
48
48
93
82
96
64
123
58
26
70
64
63
35
14
111
78
50
36.2‰
38
SAO TOME
AFRICA
LIBERVILLE
FORT GENTIL
FREETOWN
MONROVIA
ABIDJAN
LAGOS
15°
10°
5°
0°
5°E

Fig. 3. Results of current-drogue measurements at the depth of the salinity maximum in the equatorial region between 15°W and 8°E. Observations made by R. V. *Pillsbury* are shown by solid arrows and observations made by R. V. *Geronimo* by broken arrows. Direction of the arrows indicate average drift of the drogue during a tracking period of about 12 to 14 hours. Average speed is given in cm/sec. East of 0° longitude, oceanographic station locations are shown by dots. The hatched area indicates the southeastward extension of the high-salinity core (with salinities in excess of 36.2 parts per thousand.) Insert shows location of survey area.

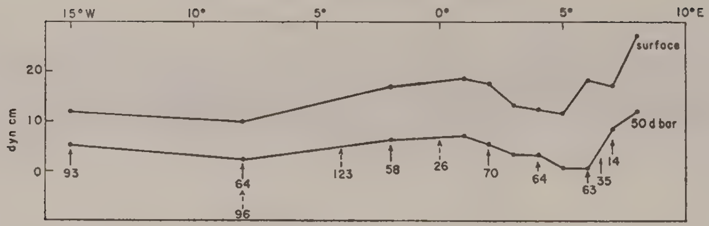

Fig. 4. Zonal slope of the sea surface and of the 50-db surface along the equator between 15°W and 8°E. The current speed in cm/sec as observed by drogue measurements at the depth of the high-salinity core is shown at the proper position under the graph of the 50-dbar surface. Solid arrows indicate *Pillsbury* observations and dashed arrows *Geronimo* observations.

ally terminates near 7°E at about 1½°S. The vertical salinity gradient is extremely strong in the upper layer and continues to increase when approaching the inner part of the Gulf of Guinea. East of 5°E the salinity increases from less than 32.5‰ at the surface to 36.2‰ at a depth of 50 meters. Although Figure 2 indicates a close-off of the 36.2‰ isohaline near 13°W, the meridional section between 2°N and 2°S along the meridian of 15°W shows that salinities of 36.2‰ and more were present south of the equator between about 15′S and 50′S.

Results of current-drogue observations are summarized in Figure 3. With the exception of

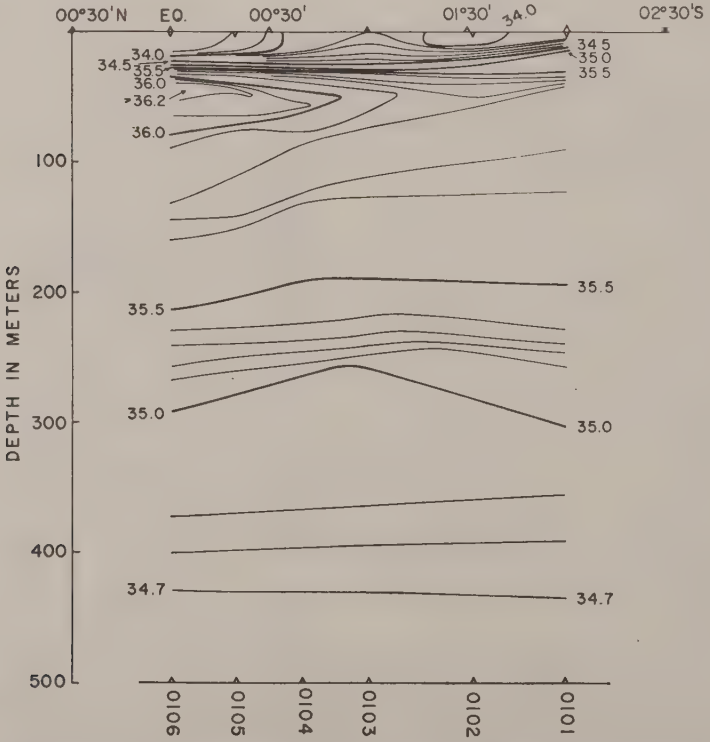

Fig. 5. Salinity section between equator and 2°S along 6°E, April 21, 1964. Station numbers are given along the bottom line of the section. Salinity in parts per thousand.

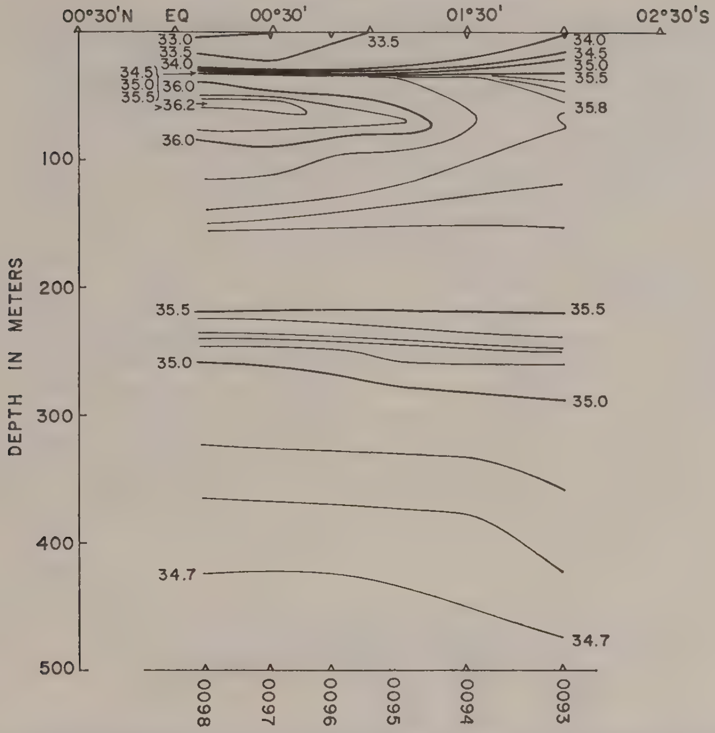

Fig. 6. Salinity section between equator and 2°S along 6°32′E, April 9, 1964. Station numbers are given along the bottom line of the section. Salinity in parts per thousand.

one measurement at 4°W (current to the NE, 123 cm/sec), the currents in the immediate proximity of the equator at the depth of the salinity maximum (see Figure 2) are more or less due east, although their speeds vary considerably.

There is evidence that the Equatorial Undercurrent is, at least to some degree, associated with a zonal slope of isobaric surfaces from west to east. Dynamic heights of the sea surface and of the 50-dbar isobaric surface were computed from the observed mass distribution with reference to the 500-dbar surface. From Figure 4 it is seen that the general slope of the sea surface and of the 50-dbar surface between 15°W and 8°W is downward from west to east and then upward between 8°W and about 1°E, although the stations west of 2°W are too far apart in distance and time to permit us to determine the zonal slope variations with the desired accuracy. However, to the east of 0° longitude the details of slope variation seem to be fairly well established. Near 1°E the slope reverses again and is downward from west to east until, finally, between 5 and 6°E (near the island of São Tomé), a steep rise of the isobaric surfaces toward the African coast is observed.

The speed of the Equatorial Undercurrent as shown in Figure 3 is plotted in Figure 4 at the proper positions along the equator. There is some evidence that the current slows down in regions where the slope is upward from west to east and accelerates or maintains its speed in regions where the slope is downward from west to east, which is the slope that might be expected to act as a driving force for this current. It should be noted that the *Pillsbury* current measurement at 15°W and the *Geronimo* current measurement at 8°W (Figure 4) were taken simultaneously. The observed speeds were 93 cm/sec and 96 cm/sec, respectively.

The longitude of the final point of slope re-

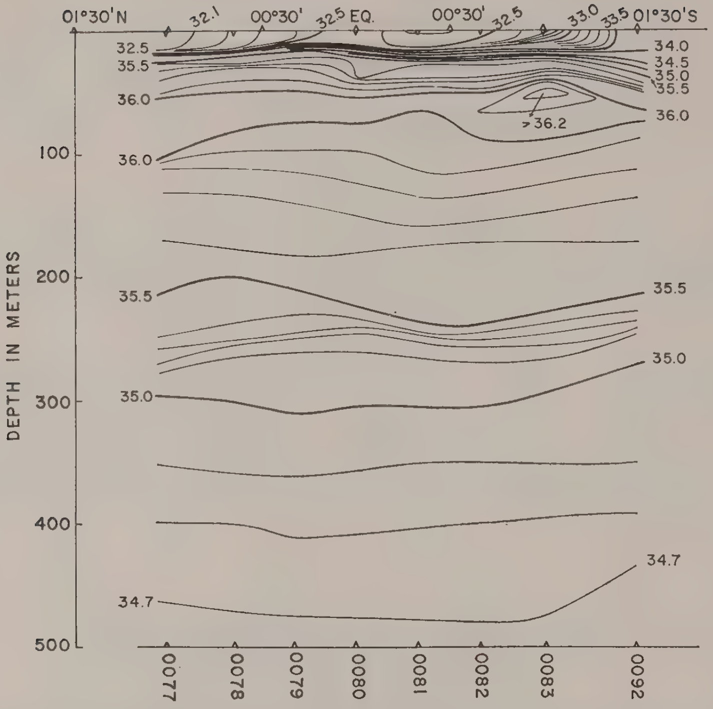

Fig. 7. Salinity section between 1°N and 1°30'S along 7°E, April 15–16, 1964. Station numbers are given along the bottom line of the section. Salinity in parts per thousand.

versal near 5°E (isobaric surfaces rising toward Africa) appears much farther to the east than can be concluded from observations taken during the late fall. Dynamic heights of isobaric surfaces along the equator with reference to the 500-dbar surface were computed from a closely spaced oceanographic section completed in November 1958 by the R.V. *Crawford* (*Crawford* stations 459–503; *Fuglister* [1960]). This section follows the equator from the inner part of the Gulf of Guinea to South America. It indicates a general downward slope of the sea surface from west to east between South America and about 7°W longitude. Between 7°W and the coast of Africa the sea surface slope rises from west to east by as much as 9 dynamic centimeters [*Neumann,* 1965].

Since the slope reversal is probably related to winds blowing toward Africa, the more easterly position of the reversal point during Equalant III may be explained by the fact that the observations were made at the end of the doldrums season. Weather observations during the last week of the operations of *Pillsbury* clearly indicated a change of the weather, with stronger SW winds and rain as contrasted to calms and occasional tropical rain showers during the preceding doldrums season. This change probably indicates the beginning of the monsoon season.

It can be expected that with a further development of the monsoon season the piling up of water against the African coast continues and that the slope reversal point moves farther westward, as can be concluded from the *Crawford* section in November 1958. It can also be hypothesized that this would move the termination of the undercurrent more toward the west during late summer and fall.

As *Pillsbury* approached the island of São Tomé on April 14, 1964, observations near 6°E suggested that the undercurrent would terminate just east of the island. Therefore, it seemed appropriate to closely space a series of stations to the east and southeast of São Tomé. If a high-salinity core were present in this area, it could be traced back to the equator, and current measurements could be made in the core. The first section along 7°E (see Figure 7) showed that the salinity core located at 1°6′S was found farther to the south, maintaining its maximum of above 36.2‰. A current observation at 12′S outside the 36.2‰ core indicated a current of 14 cm/sec to the east.

On the basis of these results, the next section (Figure 8) shows that the high-salinity core continued its southeastward displacement while the maximum observed salinity in the core decreased to 36.14‰. The surface salinity above the core maximum, however, increased rapidly from less than 32.5‰ at the equator to 33.7‰ at 1°12′S. A current measurement in the core of maximum salinity indicated an east-southeast flow of 38 cm/sec (see Figure 3). The speed of this current, observed 100 km west of the African coast, is still more than one-half the speed of the undercurrent recorded at 6°E.

Additional sections from the equator to 2°S at 6°00′E (Figure 5) and 6°32′E (Figure 6) were taken in order to locate the high-salinity core more accurately and to trace it back to the equator. Based on a closely spaced network of stations in the region east of 6°E, the extension of the high-salinity core to the southeast is shown by the hatched area in Figure 3.

It is interesting that the maximum salinity (>36.2‰) in the salinity core of the undercurrent can be followed without any significant decrease from 15°W to 7°E. The ability to do this is due to the close bottle spacing across the core. At station 76 (Figure 9) at 00°01′S, 06°01′E, where bottles were spaced at 2- or 3-meter intervals from 48 to 67 meters, salinity in excess of 36.2‰ occurred through a depth range of only 9 meters (57 to 66 meters).

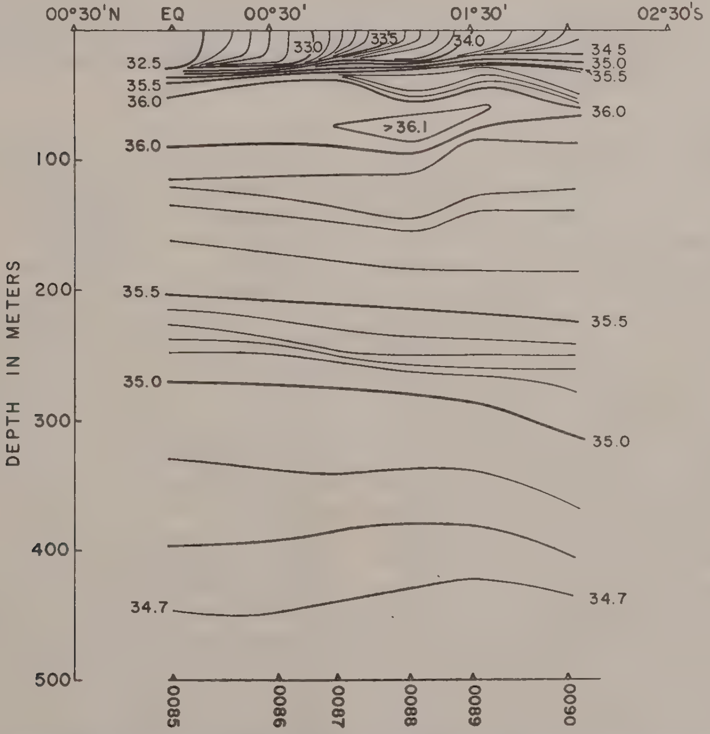

Fig. 8. Salinity section between equator and 2°S along 8°E, April 17, 1964. Station numbers are given along the bottom line of the section. Salinity in parts per thousand.

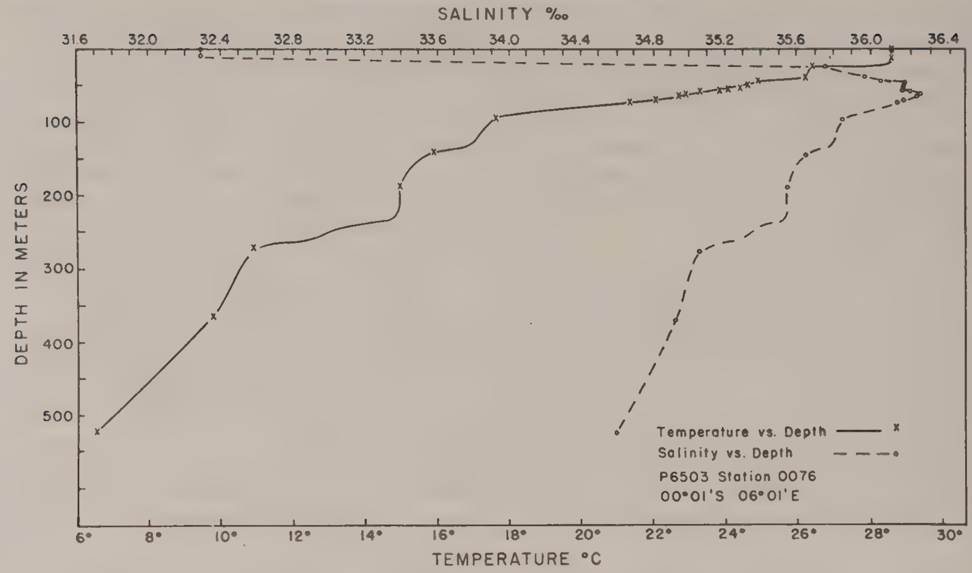

Fig. 9. Temperature and salinity distribution from surface to 500 meters at *Pillsbury* station 0076, April 14, 1964. The temperature distribution between surface and 270 meters is based on the characteristics of a bathythermogram taken at messenger time. The readings of the reversing thermometers are shown by crosses. The observed salinity values are indicated by circles; interpolation is based on the characteristics of the *T-S* diagram.

Such details in the vertical salinity distribution can easily be missed when bottles are placed farther apart. It is possible that some of the variations in salinity maximum are not real but are the result of the fact that the layer of high salinity was so narrow it was not detected with sample bottles spaced more widely apart.

Another feature of the high-salinity core associated with the undercurrent is its north-south oscillation as observed during Equalant II in October 1963 at 15°W by *Rinkel* [1963]. Also, parachute drogue observations of the Equatorial Undercurrent at 15°W during Equalant I indicate a meandering of the path of the current, causing north-south deflections from its average course toward the east. The estimated period of these oscillations is about 2½ days [*Neumann and Williams*, 1965]. This period is very close to a possible period of oscillation obtained by *Fedorov* [1965] for 'equatorial seiches.' If such oscillations continue along the path of the undercurrent until it reaches its termination area, it is possible that the current and its high-salinity water can at times be deflected into the northern hemisphere.

The fact that the high-salinity core observed in the undercurrent at the equator turned southeastward at the longitude of the island of São Tomé may be pure coincidence. The island extends from about 0°25′N to the equator, between 6°28′ and 6°45′E. The question whether the presence of this island has a direct influence on the observed oceanographic facts cannot be answered with confidence until observations are made in different seasons. It seems reasonable to attribute the disappearance of the undercurrent near 6°E and the extension of the high-salinity core from the equator southeastward to the upward rise of the sea surface toward the African coast. At the time of the Equalant III expeditions, in the middle of April 1964, the point of slope reversal of the isobaric surfaces in the upper strata (Figure 4) was indeed located near the longitude of São Tomé. It is possible that in late summer or fall the downward slope of isobaric surfaces from the innermost part of the Gulf of Guinea extends farther westward, as can be concluded for the month of November from the observations taken by R.V. *Crawford*. The effect of such changes in the absolute pressure field of the upper water layers on the Equatorial Undercurrent and its termination in the Gulf of Guinea remain to be explored in greater detail.

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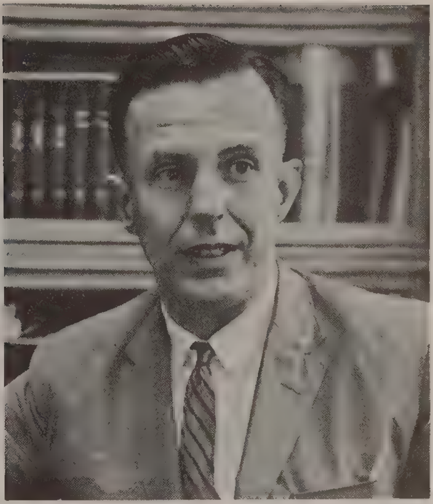
revised April 29, 1966.)

Little known to most is the role of the Bureau of Commercial Fisheries in naval oceanographic instrumentation. Guided by a "mutual support" policy, Navy and BCF work side by side on various aspects of instrumentation projects, ranging from Navy's Man-in-the-Sea program to cooperative data collecting networks.



—DATA

Need For Specialized Instrumentation Pursued By BCF

INTERVIEW WITH
DR. JULIUS ROCKWELL, JR.
Chief, Oceanographic Unit
Bureau of Commercial Fisheries

The mysterious realm of Neptune's kingdom has long been the focal point for Dr. Julius Rockwell. Graduating with a B.S. in zoology from the University of Michigan, Dr. Rockwell enlisted in the Navy in 1940. After training in naval engineering and receiving his commission, he served aboard the attack carrier USS LEXINGTON, *where he was awarded a letter of commendation for his services as engineering repair party leader. During the war he also served aboard the* NEVADA, USS BARNES, *and* FANSHAW BAY.

Returning to his alma mater in '46, he worked on Alaskan salmon research for the University's Fisheries Research Institute in Seattle. Affiliated with the Fish and Wildlife Service also in Seattle from 1954-1961, he developed an electric fish counter and other instrumentation. He received his Ph.D. in fisheries from the University of Michigan in 1956.

For the past five years Dr. Rockwell has served as Chief of the Oceanographic Unit for the Bureau of Commercial Fisheries, coming from Seattle in '61 to coordinate the Government-Industry Oceanographic Instrumentation Symposium, for which he received a superior performance award.

Dr. and Mrs. Rockwell are quite enthusiastic skiers and during the season enjoy taking off to the mountains in Maryland and Virginia. He's also quite fond of scuba diving and says the West Coast is particularly good for the sport.

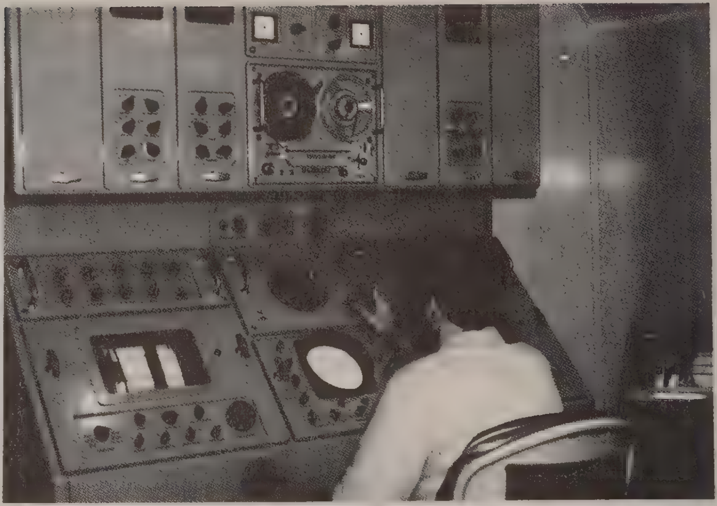
Q. Is the $900,000 assigned to the Bureau of Commercial Fisheries in Fiscal Year 1967 for oceanographic instrumentation adequate for your program in this area?

A. The $900,000 makes some provision for development, servicing, and outfitting of laboratories, bases, and vessels. It is adequate for the modest program underway.

Q. Could you tell us the purpose of the fishnet bathykymograph, the new instrument now under development, and how it will be used?

A. The fishnet bathykymograph (FBK) will measure the "catch-per-unit-of-effort" in the New England trawl fishery. Trends in catch-per-unit-of-effort provide information on whether stocks of fish are increasing or decreasing. Where geographical limits of stocks are known, it contributes information necessary for management regulations. Catch statistics are obtained from landing receipts. The measure of fishing effort has sometimes been a "boat day."

The FBK, which exteriorly resembles a headrope float, will be tied to the net when the vessel leaves port and removed upon return about 10 days later. Depth of the net is recorded against time. The catch-per-unit-of-effort statistic will be made more precise by the change from "catch per boat day" to "catch per hour of fishing." Most of these vessels make 80-120 tows per trip; it is difficult to remember or relate the number and duration of tows during the short turn-around time. The FBK record will be removed and identified for further processing.



Aboard the DAVID STARR JORDAN, *an oceanographer monitors the console of a large research sonar. Data is received from two transducers and recorded on both the strip chart (at lower left) and the magnetic recorder (center).* —BCF

Q. If you are successful in obtaining reliable instruments through this approach, what effect do you think it will have on future procurement procedures?

A. The requirements for this procedure are (1) hard specifications, (2) detailed and firm acceptance criteria, and (3) a broad need to justify the high and intense level of engineering competence required. The higher costs of specifications and proposals used rule out this method in small, unique procurements. Forthcoming standardization of observation techniques for multiship operations and monitoring networks for oceanography, meteorology, and water pollution control may be aided by this approach. The Instrumentation Panel of the ICO is preparing to recommend a similar procurement process in a multiagency requirement.

Q. How many of these instruments will be needed eventually and what is the current estimate of unit price for the instrument?

A. The initial requirement for about 200 instruments was developed by the BCF's Biological Laboratory at Woods Hole, Massachusetts. Woods Hole gathers information for the management of our New England offshore groundfish fishery as part of United States' participation in the International Commission for Northwest Atlantic Fisheries (ICNAF). The expected longevity, based on float loss records, is 5-8 years. Other (ICNAF) countries are interested, and, if the instrument is satisfactory, may wish to equip vessels similarly. Other BCF activities are also interested in its application to certain Gulf of Mexico and West Coast fisheries. State agencies and non-ICNAF nations are yet to be contacted. FBKs may be used in many commercial fisheries that drag gear over the bottom, and possibly others. The eventual world need is not known, but may be large. It is estimated the price will be under $500 per unit.

The DAVID STARR JORDAN *is the Bureau of Commercial Fisheries' mainstay research vessel. The ship, commissioned in October of last year operates from the BCF research center near La Jolla, California.* —BCF

Q. Is the Bureau of Commercial Fisheries receiving support from Navy and other agencies in the instrumentation area? How are they supporting you and how might they contribute more to your effort?

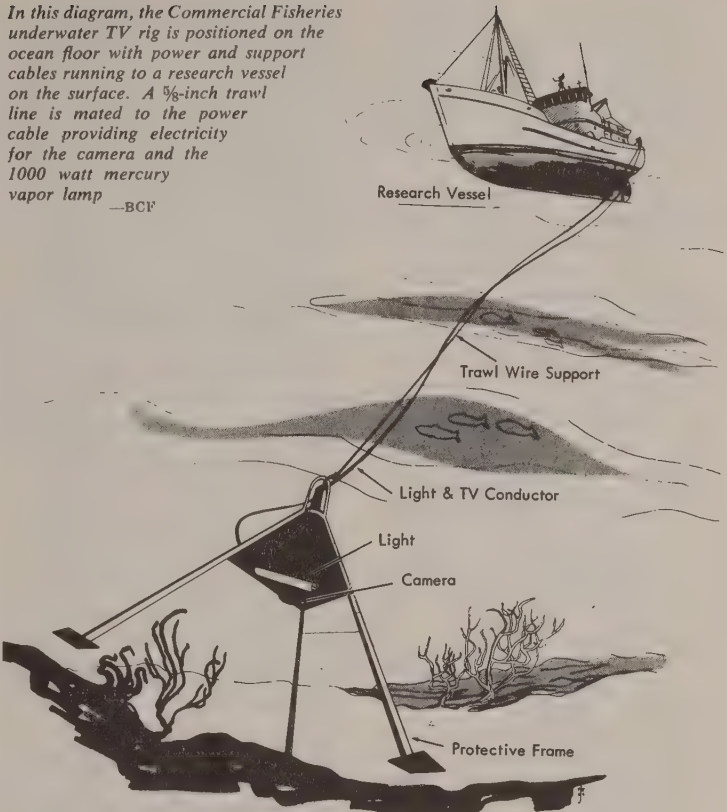
A. Yes. BCF cooperates with all agencies sharing common instrumentation problems. Bilateral or multilateral agreements are made where problems of mutual concern are involved. Mutual support is the guideline.

For instance, the U.S. Naval Oceanographic Office (NAVOCEANO) tests and calibrates reversing thermometers for some of our laboratories on a reimbursable basis. NAVOCEANO also has a reimbursable program management agreement for the development of the above-mentioned FBK. This five-task service includes advice on specification preparation and proposal review, monitoring the manufacturer's quality assurance program, supervising tests, and recommending action regarding acceptance.

Agreements have been made with the U.S. Coast Guard for two of our buoy programs. Off Cape Cod, standard Coast Guard buoys are being deployed and recovered by Coast Guard vessels. The five-buoy array has thermographs placed in concrete anchors. In the North Pacific Drift Buoy Program, Coast Guard has located and identified the radio transponding buoys on routine surveillance flights.

The North Pacific Program is participating with NASA's Interrogation, Recognition, and Locating Subsystem experiment (IRLS). BCF is purchasing a platform module as part of feasibility study of this method to locate and obtain data from drifting buoys. Our Seattle Laboratory is also obtaining a receiver for the Navy Navigational Satellite System in a multiagency procurement managed by ONR. Satellite signals received by the buoy, will, on interrogation, be radioed directly to the BCF station (KAB) along with other oceanographic data. The location of the buoy will be determined at Seattle by the Navy-designed equipment.

A large, cooperative data collecting network is now operating in the Pacific. BCF is collecting synoptic oceanographic data from buoys, merchant ships, fishing vessels, and oceanographic vessels. We supplied our near surface reference temperature measuring device and some expendable bathythermographs (XBTs) and auxiliary equipment. Navy has loaned additional XBT recorders and launchers, more conventional bathythermographs, and a winch. Navy also loaned BCF selected radio communications equipment for test and evaluation on commercial fishing vessels, because of the major communications problem of getting information from ship to shore. In return, BCF is supplying oceanographic data on a continuing basis to Fleet Numerical Weather Facility, Monterey, key to this system, through BCF-licensed radio station WWD on Scripp's campus at La Jolla. The Weather Bureau contributes extensive marine weather observations from about 1800 ships. Users of this data are ESSA for weather predictions, Navy for its ASWEPS system, BCF for scientific studies in fishery oceanography, and others. Last August, Northeast Pacific sea surface temperature data were contributed by many sources, including those from seven foreign countries. This overall network is being developed. Much of our work is providing information on the application of new subsystems being evaluated under operational conditions.



In this diagram, the Commercial Fisheries underwater TV rig is positioned on the ocean floor with power and support cables running to a research vessel on the surface. A ⅝-inch trawl line is mated to the power cable providing electricity for the camera and the 1000 watt mercury vapor lamp —BCF

This synoptic work was started in 1952 to determine the relationship between fish occurrence and temperature in the North Pacific. It would have been difficult for us to have advanced into the present, real-time phase alone. Fishery forecasting is going to become essential to the efficient harvesting of ocean resources.

The Bureau is participating in the Sealab III phase of Navy's Man-in-the-Sea program. Three BCF divers are being trained with Navy teams. Two will participate. Navy is supplying training, diving equipment, habitat space, and logistics; BCF is assisting by managing marine biological aspects and supplying tools to conduct its unique tasks.

During BCF's rental of the submersible, ASHERAH, off Honolulu, Navy provided essential standby rescue teams.

There are working arrangements between the Tropical Atlantic Biological Laboratory in Miami and ESSA on air-sea interface studies.

The David Taylor Model Basin provide its facilities for extensive hydrometric examination of plankton samplers by joint teams from BCF, Model Basin, Industry, and Institutions. It is also conducting a contracted feasibility study of a high-speed nekton sampler for our Tropical Atlantic Biological Laboratory and provides tests and calibration services.

NASA's Spacecraft Oceanographic Project, under a working agreement with the U.S. Naval Oceanographic Office and with actual participation by the Bureau of Commercial Fisheries, is supporting our contribution of scientific and operational requirements for fisheries.

Navy supplies information on oceanographic activities and aids in many minor ways too numerous to enumerate. In brief, support has been excellent at the lower levels.

Further support of the Bureau's contribution of data to the ASWEPS network could be mutually beneficial. Also, the Bureau is short of shiptime for plankton gear development in connection with acoustic surveys and to improve our capability in plankton pattern recognition.

Q. In terms of funding, what area of oceanographic instrumentation is receiving greatest emphasis at BCF?

A. We are concerned with the application of underwater acoustics to fisheries research, management, and operations.

There is a definite trend toward the "dunking types" of instrument clusters. These provide continuous profiles, enable us to take water samples at will, and free personnel for other operations. A conventional oceanographic station and a fishing operation are both "all hands" efforts. We need to do them simultaneously.

Monitoring equipment for offshore buoys and fixed estuarine stations and sensors to measure physical, chemical, and biological characteristics are desired. Demand may be expected to increase as instrument availability time and operational and maintenance simplicity are achieved.

Many of our new development efforts are being directed toward determining the requirements of instruments that need to be developed and operational studies on the capability of available equipment to our needs. These include communicating, computing, and recording equipment for ships, buoys, fixed stations, and shore facilities. We continue to assist industry by providing its engineers opportunity to evaluate progress at sea when instruments concerned are of mutual interest.

Q. Are you now using expendable bathythermographs for obtaining information on the ocean's pattern? Do you think this instrument will be used extensively by BCF in coming years? How extensively?

A. BCF has used expendable bathythermographs (XBTs) since July 1964 when a profile was made of the Dakar Shelf temperatures. Tests are still limited to operational situations to determine their usefulness and applicability to fisheries. This instrument promises to provide fast and efficiently obtainable pictures of thermal structure to a greater depth at maximum convenience and at closer time intervals than other methods. If our cost per cast can be kept below $10, then it would be useful to our research vessels.

Our Stanford Laboratory is determining the feasibility of using merchant crews of ships of opportunity to gather data with XBTs. In this test, the Matson Navigation Company's vessel, CALIFORNIAN, takes an oceanographic section between San Francisco and Hawaii every 15 days on a continuing basis. Early work indicates that these devices may also be useful to the fishing industry where a local knowledge of layer depth is pertinent to fishing operations.

The Bureau desires that the final overall system will meet fishery operational and research requirements as well as those of ASWEPS and ESSA. If these requirements are met, then application could be very extensive.

Q. You have been conducting a cooperative effort with the NASCO Panel on Biological Methods and with industry to determine the effectiveness of present plankton sampling techniques. What is the status of this program and will a new generation of plankton sampling devices evolve from this effort?

A. Improvement of plankton measuring systems is required before they can be used profitably for large, multiship operations and on ships of opportunity. In 1963, a large cooperative effort was started involving scientists from four of our laboratories and other members of the Biological Methods Panel of the National Academy of Sciences' Committee on Oceanography (NASCO). Members came from industrial laboratories and nonprofit institutions. They worked with a coordinating subcommittee of ICES-SCOR-UNESCO, and an FAO group. The purposes of this effort have been to define the requirements for a new generation of plankton samplers and to standardize methods of reporting. The following steps are largely completed and the results are either published or are in press:

(1) A literature search.

(2) Understanding of hydrodynamic characteristics of nets and synthesis of principles.

(3) Documented behavior studies of nets in operation so depth of fishing can be known and controlled.

(4) Determination of avoidance behavior of zooplankton with respect to nets.

The remaining steps include further observations with new, unique devices to verify models derived to provide a knowledge of:

(1) Distribution of discrete plankton swarms so significance of samples can be interpreted, and

(2) Requirements of organisms collected so fragile specimens may be preserved intact.

It is still early to predict final results. Possibly, a new family of nets will emerge supplemented by a family of *in situ* recorders. The former might be used for identification and sampling purposes to interpret results from plankton biomass measuring systems.

Q. How much money will BCF spend in fiscal year 1967 for direct procurement of off-the-shelf oceanography hardware?

A. $440,000 out of a total oceanography budget of $17,979,000.

Q. Are you satisfied with the support you are receiving from industry?

A. Yes and no. The rejection rate of oceanographic instruments reported earlier by NAVOCEANO appears to be low according to our experience. But a certain percentage of instruments is satisfactory. Some companies come to us early, when requirements are being developed. They wish to learn of possible application and vigorously run down requirements at shore stations and on vessels. This is rare, but I am happy to say it has proved worthwhile for them. In a second order of quality are those who sell us equipment which does not work but who are willing and anxious to correct its weaknesses. After many returns of the equipment to the company or the generally pleasant visits from the manufacturer's engineers, it does work. Nothing is charged for the service, but time is lost. The least pleasant situation is where the manufacturer admits his equipment does not meet our specifications but insists the item is satisfactory.

We are mildly surprised that there are so few companies in the first class. World fishing has been doubling every 10-12 years and is making rapid technological advances. Some of our observations give evidence of being directly applicable to fishing operations. Possibly, this lack of interest results from the American hardware industry's being so overworked by the military that it has not had time to look at fishing. Their foreign competitors have been and are being successful.

Responsibility for producing good instruments is admittedly a two-way street. This Bureau and other government agencies are striving to improve specifications and ability to insist they are met. However, until products and customer services are improved, the market will remain underdeveloped or will be lost to foreign manufacturers.

Q. What work has BCF been doing in the development of new, more powerful sonars for tracking fish?

A. We are vitally concerned with the development of acoustic fish finders. Some were derived elsewhere from sounding recorders, and others from the horizontal scanners. Sensitivity is paramount; target definition is important. Interest is developing rapidly among commercial fishermen. Fish finders are designed to display what Navy and geological sonarmen consider "noise." Larger systems use two frequencies, one for search and the other for definition.

BCF has recently purchased two powerful research sonars. One, installed on the DAVID STARR JORDAN last year, sends out a 8.5 kw. pulse. The echo returns from the target to the transducer before another is sent out. Problems of tracking an individual target increase with range. The range of this system is the best for fish finders—at least 2 miles. It is the third built in the world and the first for this country. The other system, installed last April on the TOWNSEND CROMWELL, transmits a continuous saw-tooth frequency modulated signal, and is unique. Displacement characteristics of the return transmission provide a clearer definition of a target and information on motion and direction. The maximum range, however, is less. The CTFM approach was used successfully in a much smaller system on the TRIESTE during the THRESHER search.

The other two pulse type research sonars are installed on Norwegian government vessels and are used in tracking schools, assisting fishermen in locating fish, and predicting fish movement. We are now investigating applications, limitations, and possibilities of these new research systems.

Problems and possibilities in target definition are being examined through contractural arrangement with industry and the Naval Electronics Laboratory (NEL). ■

June-September 1966

SOUND PRODUCTION BY THE AFRICAN CICHLID *TILAPIA MOSSAMBICA*

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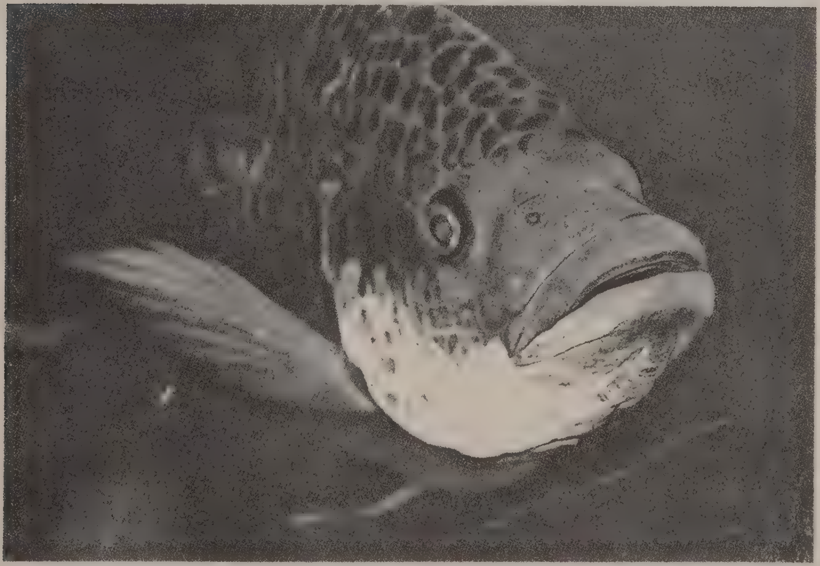
Sounds of fish have been recorded and analyzed for numerous marine species (Tavolga, 1960, 1964), but for only a few freshwater species (Winn, 1960). The African cichlid *Tilapia mossambica*. (fig. 1), a freshwater fish, has never been reported to produce intentional sound.

Freshwater fish were studied at the Bureau of Commercial Fisheries Biological Laboratory, Seattle, Washington, for underwater sounds of biological origin during experiments with recording instruments. Six male African cichlids were maintained in a 22-gallon aquarium, with a 3-inch layer of coarse gravel on the bottom. The fish produced adventitious sounds while they ate food or mouthed gravel (fig. 2). After they became accustomed to their environment, each fish constructed a shallow depression and attempted to exclude intruders. Territorial-threat behavior involved short, repetitive advances and retreats by the opponents. Intentional sounds were produced at this time (fig. 3).

Fig. 1—Tilapia mossambica. Photo by Wolfgang Bechtle.



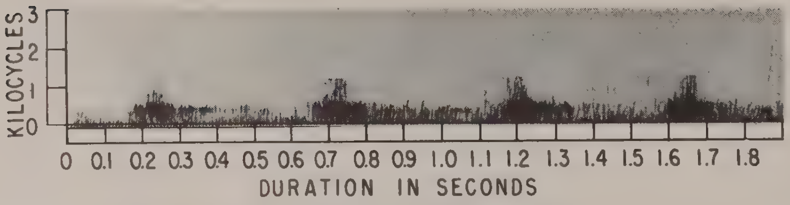


Fig. 2—Adventitious sounds produced by **Tilapia mossambica** while mouthing gravel.

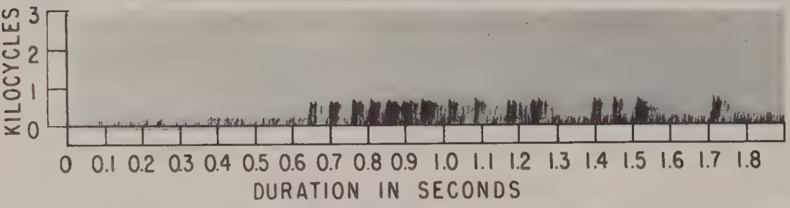


Fig. 3—Intentional sounds produced by **Tilapia mossambica** during territorial-threat behavior.

The sounds were detected with a University Model 402S microphone, waterproofed with a rubber diaphragm. They were recorded on tape with an Ampex PR-10-2 recorder-reproducer and subsequently analyzed with a Sound Spectrograph (Sonograph-Kay Electric Company). The intentional sounds were in a series of paired bursts that lasted up to 0.6 second and included individual bursts of 0.02 second. The distribution of energy was uniform in all frequency bands from 50–600 cycles per second.

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HERMAPHRODITISM IN THE SURF CLAM, *SPISULA SOLIDISSIMA*

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Oxford, Maryland

(ABSTRACT)

A single hermaphroditic surf clam, *Spisula solidissima* (Dillwyn), was found among 2,500 clams collected to determine the seasonal reproductive cycle in the mid-Atlantic bight. Standard histological techniques were used to prepare stained sections of all gonads for detailed microscopic examination. Unlike the normally dioecious gonad condition, the hermaphroditic specimen contained clearly distinguishable testicular and ovarian alveoli with developing germ cells of both sexes. The rarity of hermaphroditism in the surf clams is discussed in relation to this condition in other pelecypods.

PITAR MORRHUANA, NEW HOST FOR MALACOBDELLA GROSSA

By JOHN W. ROPES

Fishery Biologist, U. S. Fish and Wildlife Service, Bureau of Commercial Fisheries, Biological Laboratory, Oxford, Maryland

The morrhua venus, *Pitar morrhuana* Linsley, has heretofore not been reported as a host bivalve for *Malacobdella grossa* (O. F. Müller), a widely distributed commensal nemertean. Coe (1943) reported 9 pelecypod species on the European coast and two on the Pacific coast as hosts for the nemertean, but none are of the genus *Pitar*. His monograph lists the nemertean as an inhabitant of the mantle cavity of northern quahogs, *Mercenaria mercenaria,* soft-shell clams, *Mya arenaria,* and occasionally American oysters, *Crassostrea virginica,* from the Atlantic coast. A fourth bivalve host along the Atlantic coast was recorded by Porter (1962), who found a very high incidence of *Malacobdella* in southern quahogs, *Mercenaria campechiensis,* off North Carolina. McCaul (1963) listed no additional hosts in recent collections from the marine and estuarine waters of Virginia. The fol-

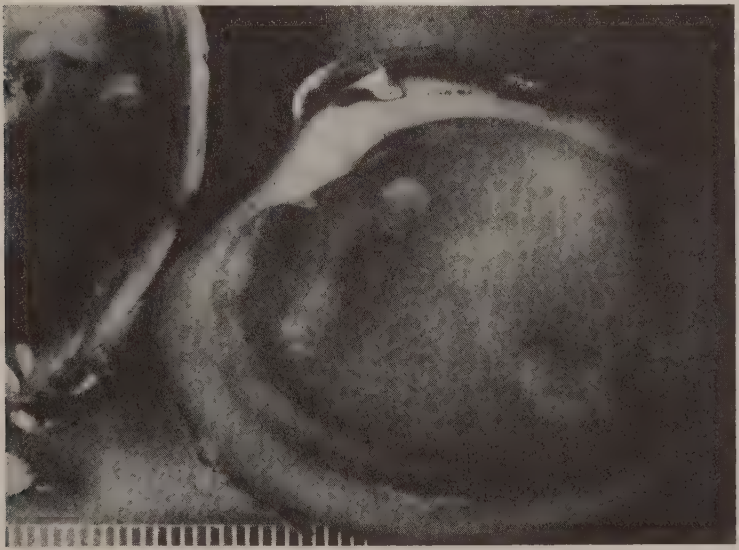

Figure 2. The nemertean *Malacobdella* attached to the mantle of *Pitar.* The scale in the lower left corner of the photograph is in millimeters.

lowing is a record of the fifth bivalve host for *M. grossa* along the northwestern Atlantic coast.

Pitar were obtained in the summer of 1964 from catches by commercial and research vessels fishing for Atlantic surf clams, *Spisula solidissima,* off the New Jersey coast. The commercial hydraulic dredges used take large quantities of live bottom fauna, some bottom sand and mud, and debris in a single tow; a similar dredge was used to collect materials for the study of *Malacobdella* in Nantucket Sound, Mass. (Ropes, 1963). *Pitar* and several other bivalve species were sorted out of the dredge catch from New Jersey. After they were measured and opened, a thorough search was made on the surface of the mantle and body mass. Only *Pitar* contanied the nemertean. *M. grossa* occurred in 6 of 42 *Pitar* caught at 15 stations (Fig. 1). The incidence of infection was 14%. Shell-length measurements of the 42 *Pitar* ranged from 32 to 52 mm. and averaged 42 mm.; *Malacobdella* occurred in specimens 33 to 45 mm. long. Several photographs taken within a few minutes after opening the clams showed that the sucking discs of all 6 nemerteans were attached to the mantle (Fig. 2).

Each host contained only a single nemertean.

The *Pitar* were dredged from water depths of 40 to 120 ft. (*ca.* 12.2 to 36.6 m.). Clams containing the nemertean were in depths ranging from 84 to 120 ft. (*ca.* 25.9 to 36.6 m.).

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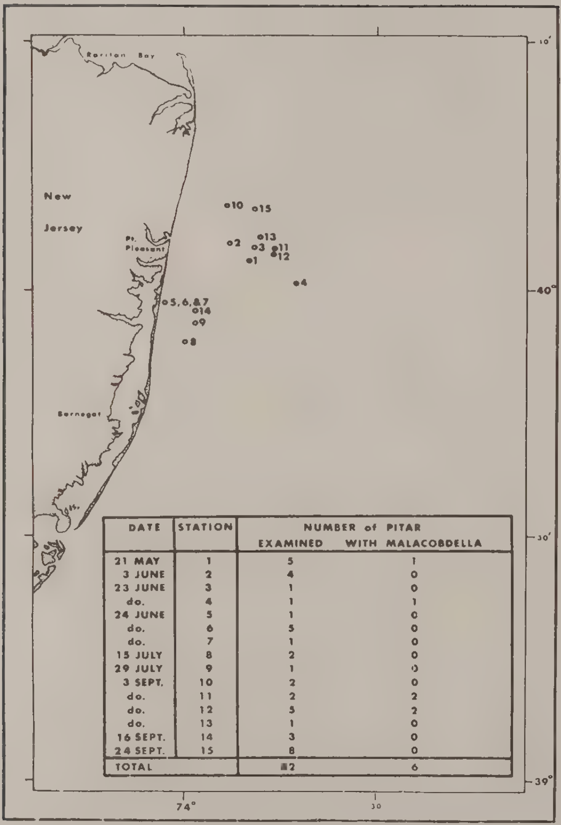
Raritan Bay
New
Jersey
Pt.
Pleasant
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o10
o15
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o1
o4
o5, 6, & 7
o14
o9
o8
10'
40°
30'
39°
74°
30

DATE	STATION	NUMBER of PITAR	
		EXAMINED	WITH MALACOBDELLA
21 MAY	1	5	1
3 JUNE	2	4	0
23 JUNE	3	1	0
do.	4	1	1
24 JUNE	5	1	0
do.	6	5	0
do.	7	1	0
15 JULY	8	2	0
29 JULY	9	1	0
3 SEPT.	10	2	0
do.	11	2	2
do.	12	5	2
do.	13	1	0
16 SEPT.	14	3	0
24 SEPT.	15	8	0
TOTAL		[illegible]2	6

Figure 1. Localities of collection of *Pitar,* and numbers that contained *Malacobdella grossa,* New Jersey coast, 1964.

The Burrowing Activities of the Surf Clam

by John W. Ropes and Arthur S. Merrill, *U. S. Bureau of Commercial Fisheries, Biological Laboratory, Oxford, Maryland.*

Our need for knowledge about the formation of offshore beds of the surf clam, *Spisula solidissima* (Dillwyn), and the rate of burrowing of marked clams in re-establishing themselves in the beds has led us to make observations wherever we find near-shore clam populations. Beaches along the mid-Atlantic coast offer a unique opportunity to observe the locomotive activities of the surf clam, as large numbers are found frequently in the surf zone.

Surf clams, especially small ones, are often uprooted by strong water currents that shift the sand. If the current is sufficiently strong, the clams themselves may be transported a considerable distance until the current spreads out and is reduced in velocity and they can burrow in again. On the open beaches at Sandy Hook, New Jersey, and Wallops Island, Virginia, we have noticed occasional temporary long-shore bars and rip channels produced by strong currents. The small clams tend to aggregate in large numbers along the edges of these bars where the current is relatively weak. Underwater currents may be a major factor in offshore bed formation which eventually concentrate clams in enough numbers for fishermen to harvest them economically.

Although the processes leading to aggregation and resultant bed formation are intriguing, this paper will not dwell further upon the subject. The preceding brief account was given to provide a background so that the reader can understand more readily the reasons for studying burrowing activities.

Watanabe (1965) recorded marked fluctuations in the movement of sand in the surf zone even during short periods of time; the degree of fluctuation depends on the force of shallow-water waves and winds that produce bottom turbulence. We have often observed the effect of bottom turbulence on small surf clams in the beach surf zone, commonly finding them dislodged by sand movement, then tossed about by wave action. When the action lessens momentarily, the clams attempt, usually successfully, to dig in again.

An understanding of the burrowing behavior of the clams is important because burrowing is the means by which they re-establish themselves in the bottom after they have been dislodged. More important to the fishery biologist, however, is to know whether all sizes of surf clams, even large

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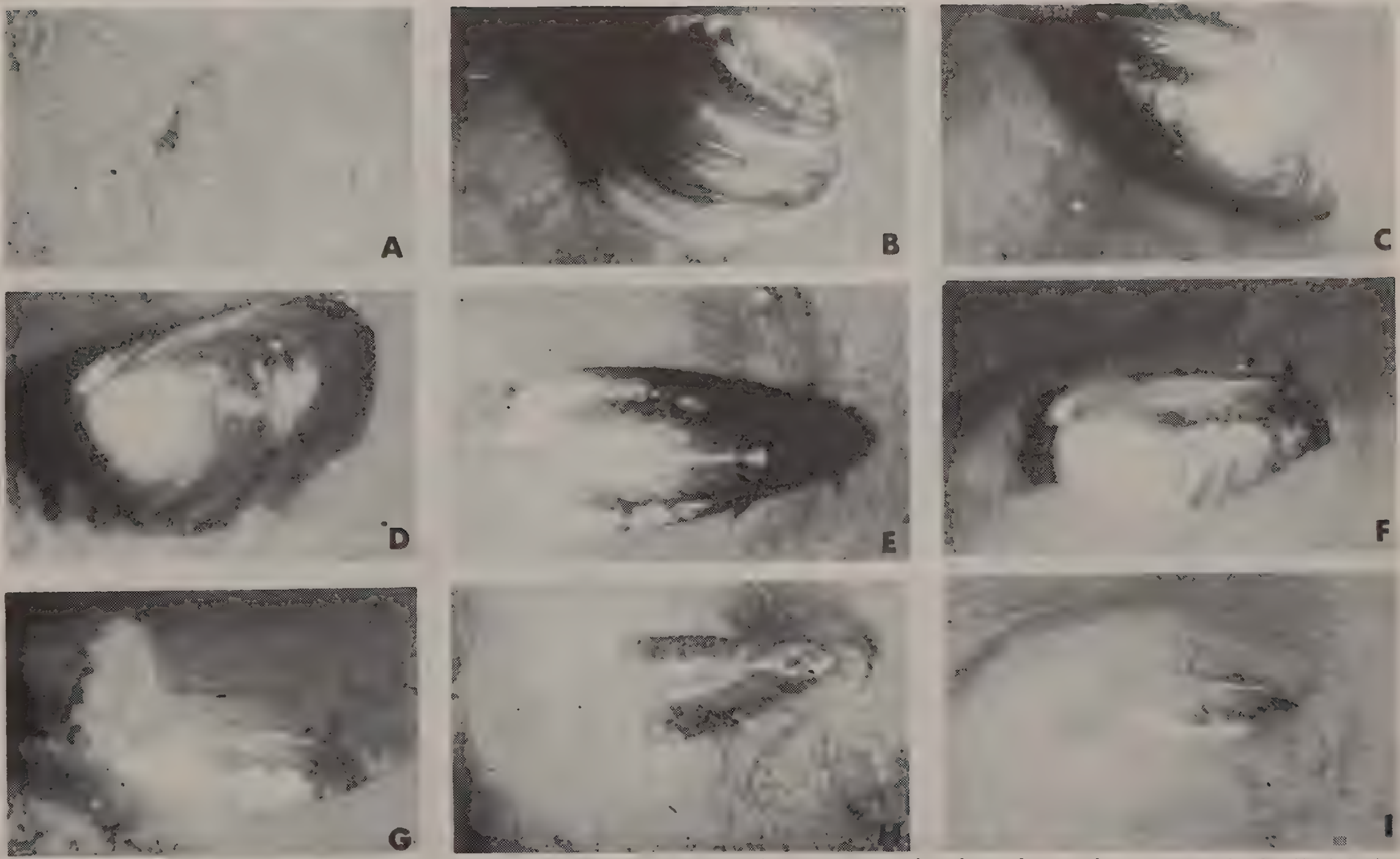


Figure 1. A series of underwater photographs showing an adult surf clam burrowing into the sand.

photos by Bradford Luther

adults, promptly dig in again when returned to their natural environment after being marked for growth and population studies. Belding (1910) briefly described burrowing of the surf clam but many important details were not included.

In this paper the jetting action which accompanies burrowing by the surf clam is emphasized since this action significantly alters the substrate at the burrow site and is not well-documented in the literature. Armstrong (1965) described burrowing activities for bivalves but made no mention of jetting action by any of them. Trueman (1966) noted the ejection of water from the mantle cavity and subsequent liquification of the sand adjacent to the shell; however, his study principally concerned the dialation of the foot to anchor the clam prior to the muscular contractions that pull the clam into the burrow. We describe and illustrate the explosive force of the jet action and its role in the clam's ability to burrow rapidly into the substrate.

For this report, we observed the burrowing of large and small clams,—in the natural environment using SCUBA and in the laboratory using aquaria. The two types of observations complement one another. On the ocean bottom one can observe burrowing activities only from above the substrate; in aquaria it is possible to see the burrowing above and below the sand surface. The latter observations explain some of the activities seen in the natural environment.

The photographs in Figure 1 were taken underwater off Truro, Cape Cod, Massachusetts, in a depth of 20 feet in August 1965. They were taken by Bradford Luther of Fairhaven, Massachusetts, an experienced diver who collects specimens and makes observations for us from time to time. On this occasion he was gathering surf clams for our use in gametogenesis studies. An Argus C-4 camera with a Highlander strobe (electronic flash) and Ectachrome-X film produced the colored transparencies from which these black-and-white prints were made. The series shows the burrowing action of a surf clam and, together with Brad's verbal comments, provides the following description.

Figure 1A shows a hole in the sand bottom which is the only indication that a clam is present here in the substrate. The animal lives completely buried in the sand with its uppermost portion about ½-inch below the surface, but with its short siphon extended just to the surface. The siphon draws in water and food particles and expels water and waste materials—these actions produce the typical hole shown.

To capture the burrowing action on film, the diver dug out a large clam of 125 mm (about 5 inches) and placed it on its side on the bottom. Almost immediately the animal protruded its powerful foot and forced it into the substrate as seen in Figure 1B. Then, in a quick motion, it righted itself so that the hinged area and umbone were uppermost (Fig. 1C). In this position the clam made several vigorous thrusts to dig itself below the surface again as indicated in the sequence of Figure 1D through 1I. This sequence took about two minutes. Each strong thrust was accompanied by a geyser of sand which spouted upward. This sand is seen clearly in Figures 1D and 1G. When the clam was back in its normal position again (Fig. 1I) a mound of displaced sand surrounded the all-but-hidden clam. Minor water currents will complete the job of leveling the mound and covering the animal. Soon the clam is busily siphoning again and only the hole, like that in Figure 1A, is apparent.

Several details about the burrowing could not be seen in the natural environment. In particular, it was not possible to determine how the clam caused sand to spurt out of the burrow.

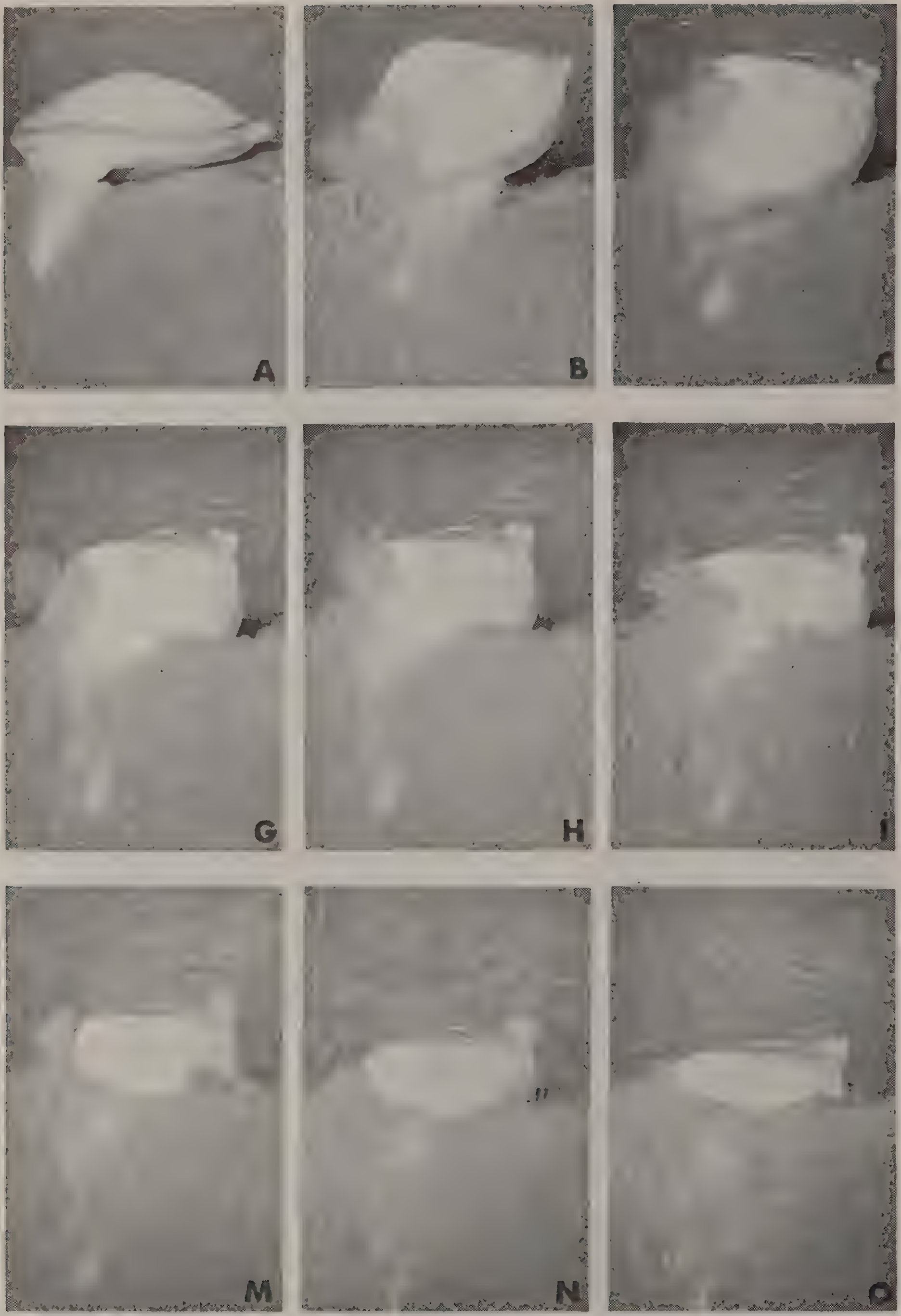
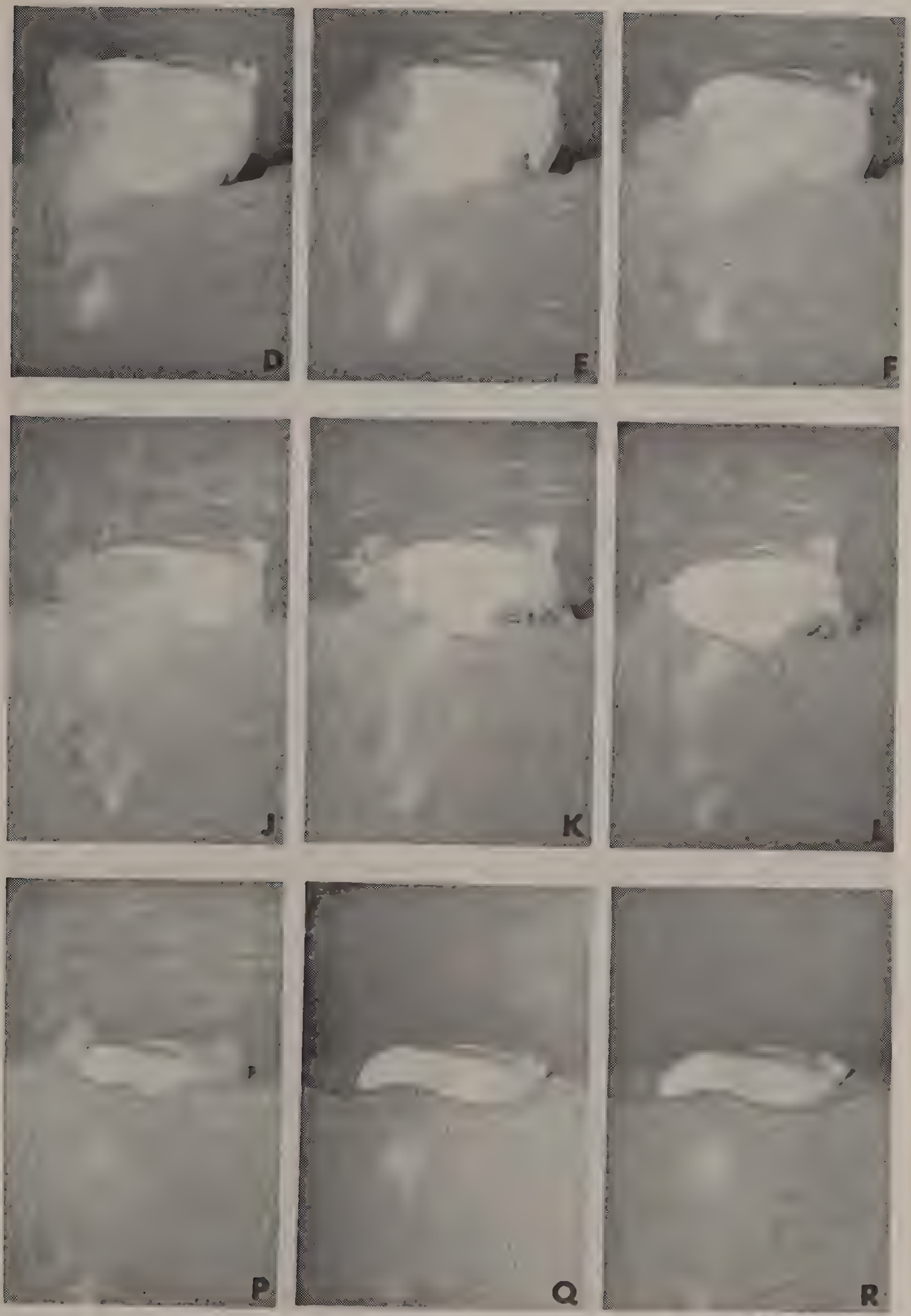


Figure 2. A series of photographs taken through an aquarium wall showing,



photos by John Ropes

in sequence, the burrowing action of a juvenile surf clam.

We duplicated this action in an aquarium using juvenile clams 50 to 75 mm (2 to 3 inches). The clams were from a population we discovered on Wallops Island near Chincoteague Inlet, Virginia, and were using to conduct studies of growth and population density. After we had acclimated some of these clams in aquaria containing sand and local sea water at our nearby substation at Franklin City, Virginia, we observed their burrowing activities. We found that when we placed several clams near the aquarium glass, one occasionally burrowed in the sand at the face of the glass where we could observe the complete action.

Figure 2 shows a sequence of the movements that a clam 65 mm (about 2½ inches) made as it sought to bury itself in the substrate. The first photograph (Fig. 2A) shows the clam on its side, its valves open, its foot extended through the opening between the mantle edges and the tip probing into the sand. When the foot reached about two inches into the substrate, it anchored and the clam, by retraction of the foot muscles, drew itself downward. At the same time, water currents produced by the clam forced sand away from an area near the foot. The mechanics of the "jet" action by the animal cannot be seen in the photographs; it is probably similar, however, to the action by which scallops jet-propel themselves through the water. The valves of the shell open wide, filling the mantle cavity of the shell with water. Muscular action brings the opposing mantles tightly together. The stored water is then forced out of a small opening produced by a puckering of the otherwise closed mantle in the area where the jetting is to take place. In the surf clam, the mantle opens in a ventroposterior part near the foot so that the stored water is ejected downward with considerable force as the clam abruptly closes its valves. The entire burrowing action is a rhythmical sequence of events. The clam opens its siphons, expands by relaxing the adductor muscles, and allows the resilium in the hinge to open the valves naturally. This action fills the mantle cavity with water. The siphons and the mantle are then closed to trap the water inside the clam, whereupon the clam abruptly draws the valves together to drive water out near the probing foot. The force of this stream of water can be judged by the billowing sand rising about the shell in the succeeding photographs (Fig. 2B to 2M) and the cylindrical hole produced adjacent to the foot. This action can be compared to the modern method of seating pilings through use of a jet stream of water to displace the substrate. Each time sand is displaced, the clam extends its foot farther into the sand and nuzzles its shell farther into the opening. The extended foot in Figure 2P had touched the solid bottom of the aquarium and the animal had, in the same motion, pulled itself downward. When the animal was unable to dig deeper, it eased upward as the sand-covered siphon in this photograph shows. After a few more attempts to penetrate deeper the clam ceased burrowing efforts and remained in the position shown in Figure 2Q and 2R.

Laboratory and field observations show that once it begins, a clam can dig in completely with about 8 to 10 vigorous movements. When we placed a clam on its side in an aquarium, it usually lay quietly for a period up to two hours, depending on previous condition factors and water temperatures, before it started to dig. We could cause a clam to start burrowing almost immediately, however, by leaving it out of water about an hour, a fact that aided greatly in setting up for observations and photography. A clam always digs in rapidly and at once when uncovered in the beach surf zone. Possibly the condition that stimulates clams to reseat themselves quickly in nature is the bouncing about they receive from the action of waves or currents. It is certainly to the advantage of a clam at the water's edge to disappear again as rapidly as possible after it has been uncovered. Repeated dislodgements of the clams are in a shoreward direction as the tide rises; many are stranded with each tidal recession. The speed of burrowing determines the number of clams that will be washed shoreward to die eventually in windrows on the beach (see Barnes 1910; Jacot 1920) or will dig in and survive. When dislodged, the clams are also vulnerable to predation by marine birds. Flocks of sea gulls are ever near small clams in distress at the water's edge; witness the many small mounds of shell fragments—regurgitations by the gulls—that form a part of the debris on the beach.

Bulloch (1965) who reported underwater field observations on a commercial surf clam bed offshore of Point Pleasant, New Jersey, noticed that the clams protruded from the sandy bottom about one-third of their body length, generally at an angle, and remarked that all clams seemed to face in one direction. Our knowledge of the burrowing habits of large surf clams leads us to believe that they usually burrow entirely beneath the surface. We have seen, however, though rarely, quantities of clams brought in by fishermen that have had algae growing on a portion of the shell nearest the siphon. These algae indicate that the clams were not completely buried. When the clam is partially uncovered, we suspect that either the bottom substrate is too hard for the clam to complete the burrow or that water currents gradually removed part of the covering material. Possibly a combination of the two factors contributes to this situation. Armstrong (1965) found definite orientation due to the forceful effect of water action on the two burrowing species, *Tivela stultorum* (Mawe) and *Siliqua patula* (Dixon). Bulloch's remark that the clams all faced in one direction suggests strong currents in the area.

Surf clams are taken commercially by a hydraulic jet-dredge operated from a clamming vessel. Powerful streams of water that spray the bottom immediately in advance of the dredge, loosen the substrate and uncover the clams so that the animals may be gathered into the dredge as it follows. It is ironic that the clam which uses the hydraulic principle in part to burrow beneath the sand is dislodged and harvested by a tool that uses the same principle.

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ABSTRACT

THE DISTRIBUTION OF "MSX" IN MIDDLE CHESAPEAKE BAY

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Within the past two years the oyster microparasite "MSX" has penetrated farther into Chesapeake Bay, at least as far north as Broad Creek on the eastern shore and Cedar Point Hollow on the western shore. Furthermore, within the past year an increase in the incidence of the parasite has been observed in areas where it has previously been found. Although mortalities as determined by fresh box-gaper counts have not been observed to be unusually high in the areas sampled, mass mortalities have been reported in other areas.

Reprint In Thomas A. Manar (editor), Proceedings, Governor's Conference on Central Pacific Fishery Resources, State of Hawaii, Honolulu, 1966.

MAJOR CHANGES IN THE TEMPORAL-SPATIAL DISTRIBUTION OF CATCH AND EFFORT IN THE JAPANESE LONGLINE FLEET

By

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ABSTRACT

The Japanese longline fishery takes a large proportion of the total Pacific Ocean catch of tunas and billfishes. The publication Tuna Fishing issues catch and effort data from a substantial portion of the Japanese longline fleet. From these, the year-to-year changes in the distribution and relative catch and effort from 1953 to early 1964 have been determined. An increasing proportion of the effort has gone into the eastward extension of the fishery. In 1953, effort was largely concentrated off Japan; by 1963, peak effort was being expended at the longitude of Baja California. Latitudinally, the chief effort in 1953 was in the North Pacific; by 1963, it had shifted to the South Pacific. Peak catches (in numbers) of yellowfin tuna (*Thunnus albacares*) have been in the equatorial western Pacific; for bigeye tuna (*T. obesus*) they have shifted from near Hawaii to the equatorial eastern Pacific. Studies of catch per unit of effort indicate that apparent abundance declines for yellowfin tuna and increases for bigeye tuna, from west to east.

INTRODUCTION

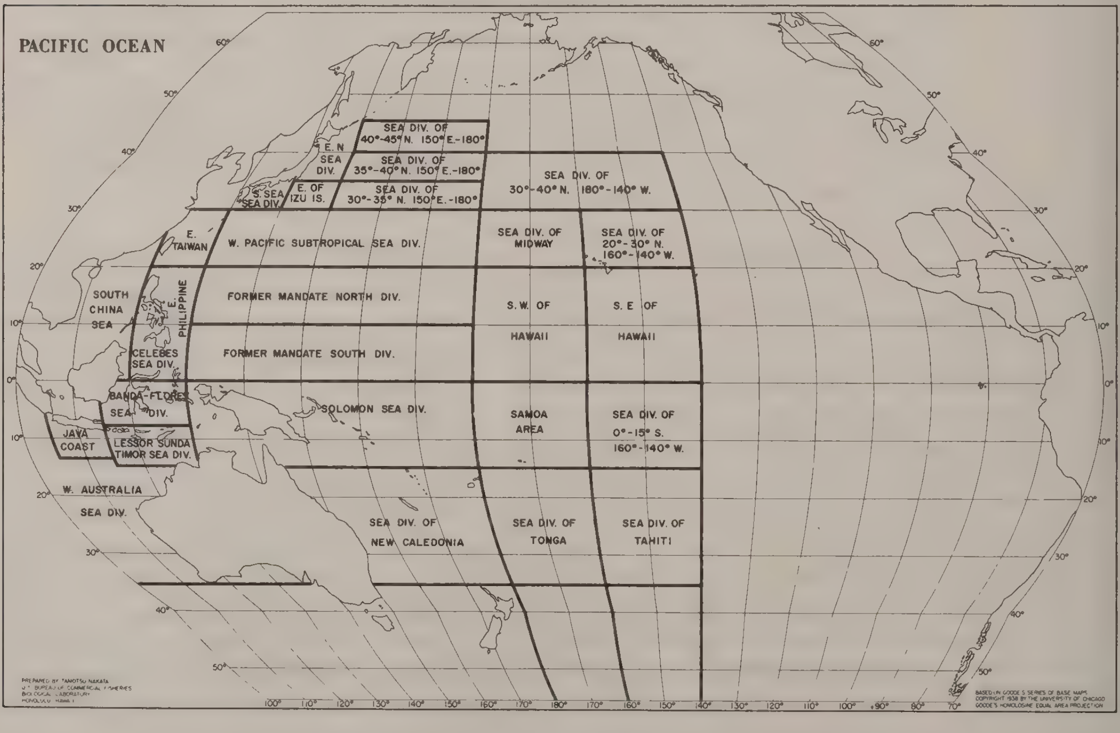
The Japanese longline fishery takes a large proportion of the total Pacific Ocean catch of tunas and billfishes. Catch and effort data from this fishery have provided a basis for inferences on the distribution and abundance of the several harvested species, thus providing source material for numerous publications. Some recent examples include: the discussion by Suda, Koto, and Kume (1963) on the apparent abundance of tunas and billfishes in the Indo-Pacific region; the consideration of yellowfin tuna distribution by Kamimura and Honma (1963); and the study of the distribution of billfishes by Howard and Ueyanagi (1965). These, as well as the well-known reports on the "average year's fishing condition" published by the Nankai Regional Fisheries Research Laboratory, emphasize seasonal distributions of catch and effort on the basis of either a single year's data or several years of data pooled together. Suda and Schaefer (1965a) and Kume and Schaefer (1966) have, however, considered in detail quarterly through annual changes for that portion of the longline fishery which occupied the eastern Pacific Ocean east of long. 130° W., from 1956 to 1963.

In this paper I emphasize year-to-year shifts in the distribution of relative catch and effort of the Japanese longline fleet for the entire Pacific Ocean from 1953 to early 1964. I have used the most abundant source of published data, that in the Japanese publication Tuna Fishing (published monthly by the All Japan Investigative Conference of Tuna, Misaki Branch, c/o Kanagawa Prefectural Fisheries Experimental Station, Misaki-machi, Miura-shi, Kanagawa, Japan).

The catch and effort data in Tuna Fishing have been given in three formats: (1) in 1953-59 the data for each species were reported by month in numbers of hooks and numbers of each species taken within an area (usually rectangular), specified by a longitudal and latitudinal boundary and included in a major fishing ground (fig. 1); (2) the data for 1960 were given in terms of catch per unit of effort (CPUE) only and are not included herein; and (3) the data for 1961-64 were given for each species by month in numbers of hooks and numbers of fish taken within specified statistical areas which are in actuality 5-degree (300^2-mile) quadrangles.

To standardize the data I transformed the pre-1960 material to a uniform 5-degree quadrangle scale. The transformation was accomplished by overlaying the pre-1960 rectangle with the post-1960 grid of 5-degree quadrangles. The portion of each statistical area that lay

Figure 1.--Statistical areas used to report catch and effort statistics in Tuna Fishing through 1959.


PACIFIC OCEAN
SEA DIV. OF 40°-45° N. 150° E.-180°
E. N SEA DIV.
SEA DIV. OF 35°-40° N. 150° E.-180°
S. SEA SEA DIV.
E. OF IZU IS.
SEA DIV. OF 30°-35° N. 150° E.-180°
SEA DIV. OF 30°-40° N. 180°-140° W.
E. TAIWAN
W. PACIFIC SUBTROPICAL SEA DIV.
SEA DIV. OF MIDWAY
SEA DIV. OF 20°-30° N. 160°-140° W.
SOUTH CHINA SEA
E. PHILIPPINE
FORMER MANDATE NORTH DIV.
S. W. OF HAWAII
S. E OF HAWAII
CELEBES SEA DIV.
FORMER MANDATE SOUTH DIV.
BANDA-FLORES SEA DIV.
SOLOMON SEA DIV.
SAMOA AREA
SEA DIV. OF 0°-15° S. 160°-140° W.
JAVA COAST
LESSOR SUNDA TIMOR SEA DIV.
W. AUSTRALIA SEA DIV.
SEA DIV. OF NEW CALEDONIA
SEA DIV. OF TONGA
SEA DIV. OF TAHITI
60°
50°
40°
30°
20°
10°
0°
10°
20°
30°
40°
50°
100°
110°
120°
130°
140°
150°
160°
170°
180°
170°
160°
150°
140°
130°
120°
110°
100°
90°
80°
70°

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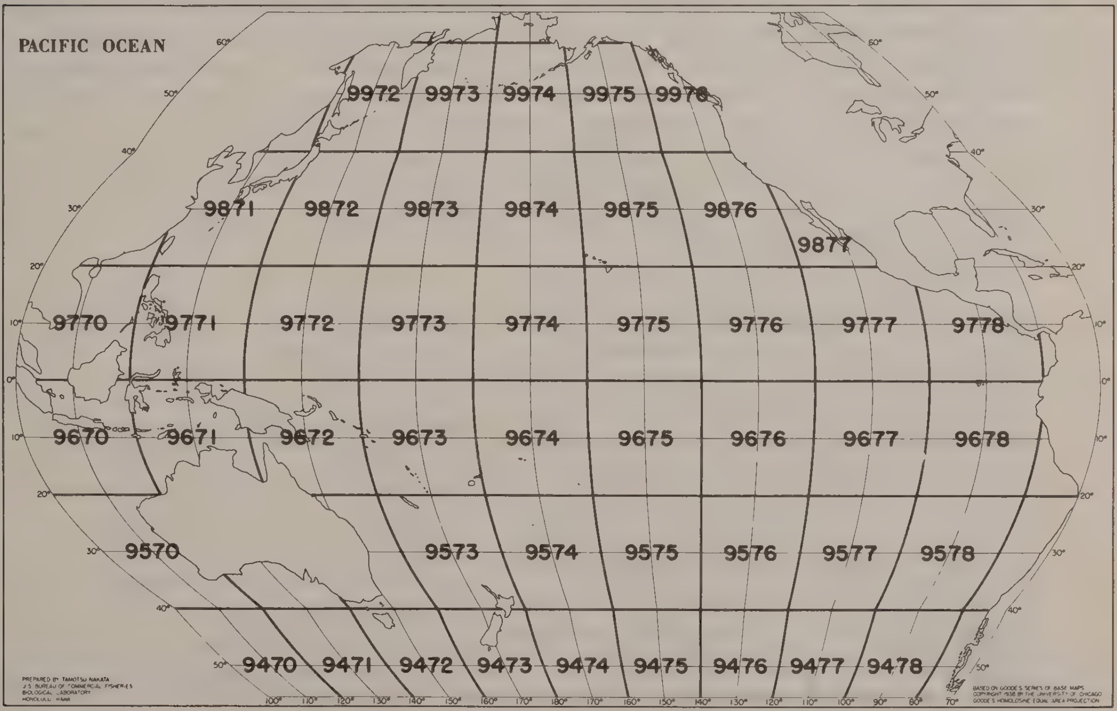
within the pre-1960 boundaries was then computed. Statistical areas that were wholly included within the earlier boundaries were taken to be 300^2 miles in area; statistical areas that were intercepted by the pre-1960 boundaries were computed as a fraction of 300^2 miles. The proportions so obtained were applied to the reported number of hooks and fish for the bounded area to obtain an estimate of the bounded area's contribution to each 5-degree quadrangle. An obvious consequence of this procedure is that catch and effort for a large area tends to be distributed evenly over many smaller areas and that the variation among these smaller areas is less than the variation which would obtain if the actual data for these small areas were available. This consequence is not serious in the context of this study, however, since large-scale changes remain discernible.

For the present survey, data were pooled in 20-degree quadrangles. (More detailed studies are planned in which the data will be examined by 5-degree quadrangles.) The location of the boundaries is arbitrary; I chose to examine 20-degree bands north and south of the Equator rather than bracket the Equator with a single 20-degree band (10 degrees north and south of the Equator). This choice placed the Hawaiian Islands at a focal point, the intersection of four 20-degree quadrangles. In considering the data summaries it must be remembered that both quadrangle size and placement of quadrangle boundaries affect the resolution and within-

Figure 2.--Statistical areas established for this study.


PACIFIC OCEAN
9972
9973
9974
9975
9976
9871
9872
9873
9874
9875
9876
9877
9770
9771
9772
9773
9774
9775
9776
9777
9778
9670
9671
9672
9673
9674
9675
9676
9677
9678
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9573
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9576
9577
9578
9470
9471
9472
9473
9474
9475
9476
9477
9478
60°
50°
40°
30°
20°
10°
0°
100°
110°
120°
130°
140°
150°
160°
170°
180°
170°
160°
150°
140°
130°
120°
110°
100°
90°
80°
70°
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quadrangle homogeneity of the data. For example, a quadrangle as large as 20 degrees might include two fishing grounds and therefore any statistics from it would be a weighted combination of the data from each. Further study is required to determine the quadrangle size that will best provide a balance between the number and the internal homogeneity of the quadrangles.

The placement of the 20-degree quadrangles is shown in figure 2. Each quadrangle is identified by a four-digit number. The first two digits, ranging from 94 in the south to 99 in the north, denote latitudinal bands; the last two digits, from 70 in the west to 78 in the east, denote longitudinal bands. Thus, a four-digit number always refers to a particular quadrangle and a two-digit number to a particular latitudinal or longitudinal band, depending on whether its first digit is a 9 or a 7.

All CPUE's in this paper are ratios of average catch to average effort rather than the average of catch-to-effort ratios. This choice was primarily based on an intent eventually to utilize ratios of averages to estimate totals. The choice of the "best" estimator for this problem needs further study.

The fact that the catch and effort data summarized in this paper are sample statistics should be emphasized. It is implicit in the discussions that the sample is representative of the population. This is presently an assumption which requires further investigation. It is known, for example, that the *Tuna Fishing* data are based on the larger boats of the fleet, particularly in the earlier years; this selection is likely to affect the representativeness of the distribution of effort more than the distribution of apparent abundance. In fact, if we make the reasonable assumption that the per-hook fishing power is the same for large and small boats, then the CPUE's based on these data should be representative of those of the entire fleet. Furthermore, one can say that the sample is large; its magnitude can be judged from figure 3, which shows the reported number of hooks for each year. The number varies from 23 million hooks in 1953 to 70 million hooks in 1962. The present paper, then, is not directly concerned with estimating total catch or total effort; catch and effort analyses are based on the percentages of total *reported* catch and effort.

Our analyses will eventually include all of the harvested species of tunas and billfishes, but at present we are concerned primarily with those species of tunas that inhabit the tropical regions, the bigeye tuna (*Thunnus obesus*), the yellowfin tuna (*Thunnus albacares*), and the skipjack tuna (*Katsuwonus pelamis*). Emphasis is placed on the bigeye and yellowfin tunas, since the skipjack tuna is not nearly as common in longline catches. Some trends in distribution of

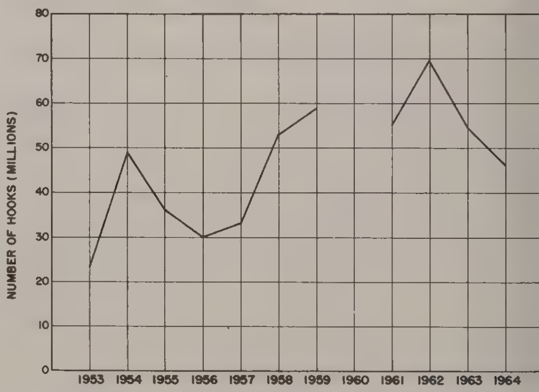


Figure 3.--Total number of hooks fished by Japanese longline fleet in Pacific Ocean, as recorded in *Tuna Fishing* each year.

albacore (*Thunnus alalunga*) are also mentioned since this species is taken in conjunction with bigeye and yellowfin tunas.

DISTRIBUTION OF EFFORT

A summary of each year's distribution of effort was obtained as a percentage of that year's total reported effort for 20-degree longitudinal bands, 20-degree latitudinal bands, and 20-degree quadrangles. The sums of the longitudinal or latitudinal percentages within a band are called zonal percentages. The word "zonal" is used as defined in Webster's Unabridged, Third Edition: "Any division of a planetary surface bounded by two encircling parallels."

The longitudinal zonal percentages of reported effort are shown in figure 4. The tendency is consistent for an eastward extension of the concentration of effort with years. In the 1953-57 period the modal value of effort centered on longitudinal band 72; in 1958 it reached band 73, but reverted to band 72 in 1959; it remained at band 72 until 1963, when it was centered in band 76. Despite a tendency for the modal value of effort to remain in band 72, the concentration of effort has spread to the east, a fact testified to by almost consistent decreases, with time, in the percentage effort expended in band 72 and almost consistent increases in the percentage of effort expended in band 76.

The latitudinal zonal percentages of reported effort are shown in figure 5. In 1953-55 the greatest concentrations of reported effort were in band 98. In 1954 and 1956, concentration of effort tended to increase in the South Pacific (band 96). After 1956, reported effort remained concentrated in band 97 until 1963, when the major latitudinal concentration of effort was in band 96.

Zonal distributions show the major trends in distribution of effort. Changes which are not parallel or normal to the meridians, however, may be to some extent obscured. To give a more detailed representation of the distribution of effort, the effort statistics for each 20-degree quadrangle and year are presented in figure 6. In addition contours of percentage effort are presented for reference in these figures; it is not intended to imply that the unit-percentage

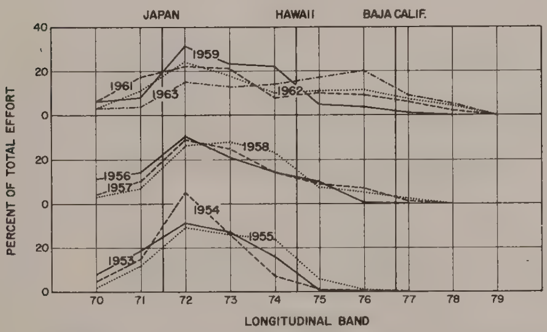


Figure 4.--Percentage of total reported annual effort (numbers of hooks) expended in each longitudinal band in 1953-63.

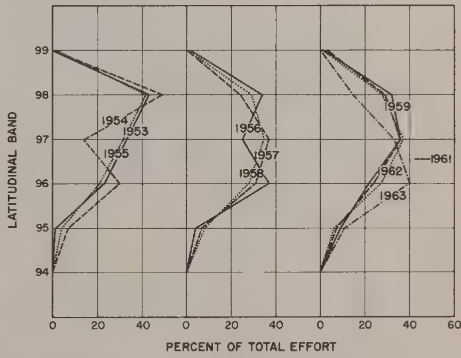
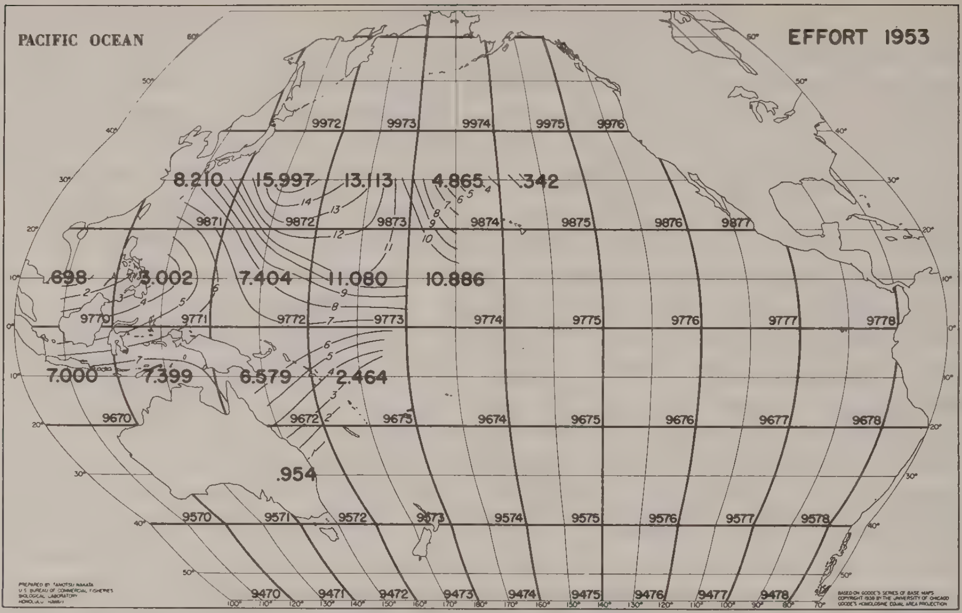


Figure 5.--Percentage of total reported annual effort (numbers of hooks) expended in each latitudinal band in 1953-63.


PACIFIC OCEAN
EFFORT 1953
8.210
15.997
13.113
4.865
.342
.698
3.002
7.404
11.080
10.886
7.000
7.399
6.579
2.464
.954
9972
9973
9974
9975
9976
9871
9872
9873
9874
9875
9876
9877
9770
9771
9772
9773
9774
9775
9776
9777
9778
9670
9672
9673
9674
9675
9676
9677
9678
9570
9571
9572
9573
9574
9575
9576
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9578
9470
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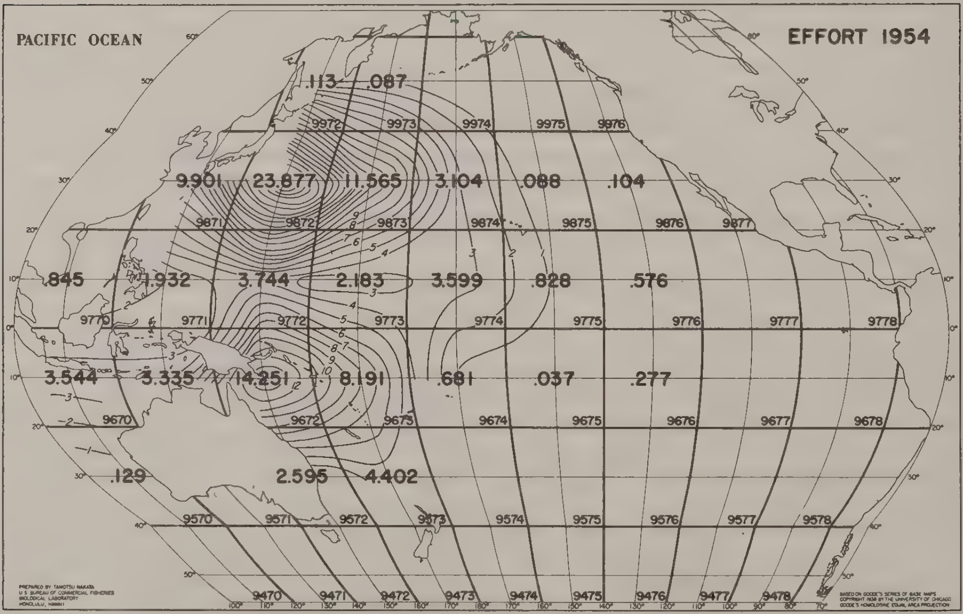
Figure 6a.--Percentage of reported total annual effort (numbers of hooks) expended in each 20-degree quadrangle in 1953.


PACIFIC OCEAN
EFFORT 1954
.113
.087
9.901
23.877
11.565
3.104
.088
.104
.845
1.932
3.744
2.183
3.599
.828
.576
3.544
3.335
14.251
8.191
.681
.037
.277
.129
2.595
4.402
9972
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9770
9771
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Figure 6b.--Percentage of reported total annual effort (numbers of hooks) expended in each 20-degree quadrangle in 1954.

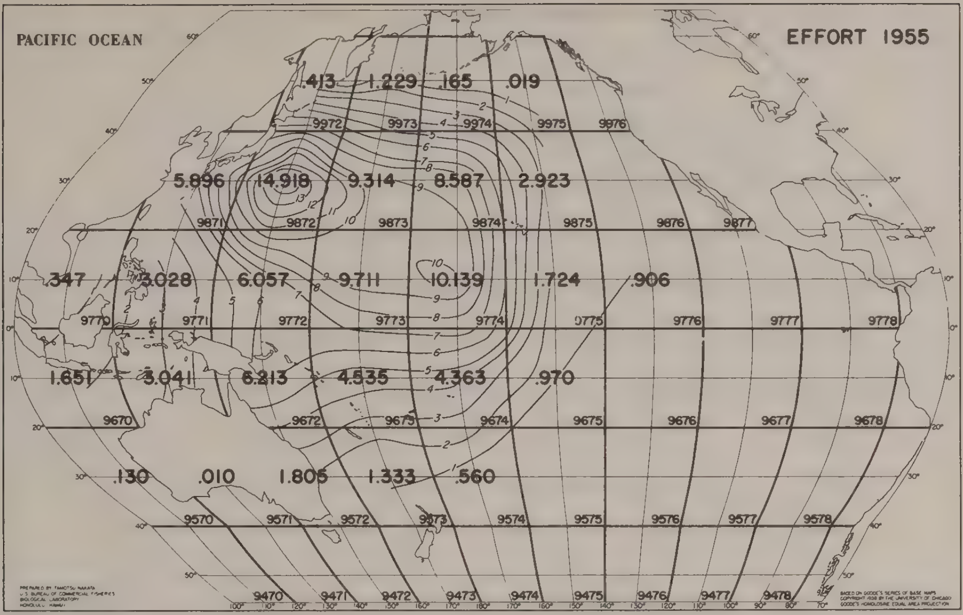
PACIFIC OCEAN
EFFORT 1955
.413
1.229
.165
.019
5.896
14.918
9.314
8.587
2.923
.347
3.028
6.057
9.711
10.139
1.724
.906
1.651
3.041
6.213
4.535
4.363
.970
.130
.010
1.805
1.333
.560

Figure 6c.--Percentage of reported total annual effort (numbers of hooks) expended in each 20-degree quadrangle in 1955.

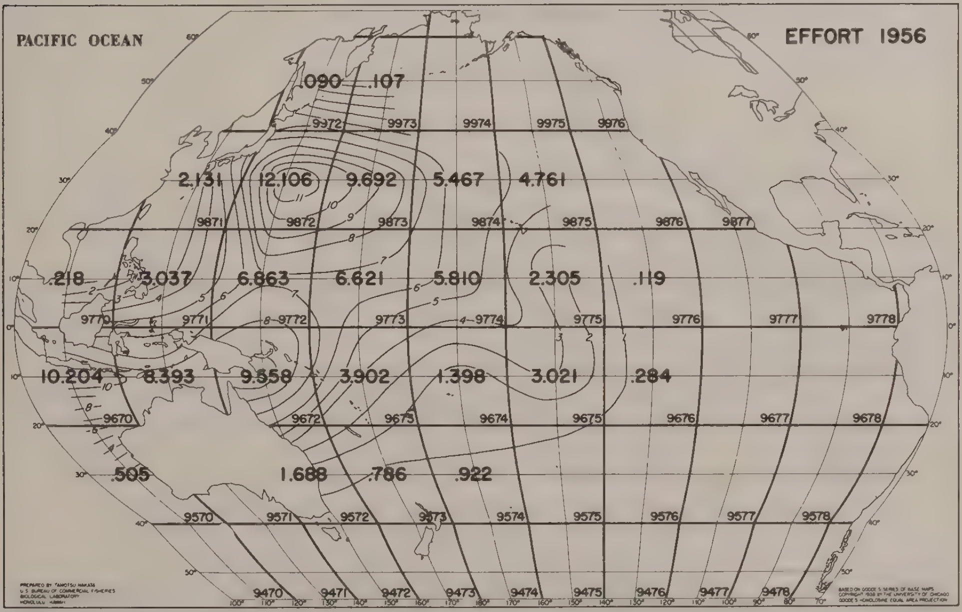
PACIFIC OCEAN
EFFORT 1956
.090
.107
2.131
12.106
9.692
5.467
4.761
.218
3.037
6.863
6.621
5.810
2.305
.119
10.204
8.393
9.558
3.902
1.398
3.021
.284
.505
1.688
.786
.922

Figure 6d.--Percentage of reported total annual effort (numbers of hooks) expended in each 20-degree quadrangle in 1956.

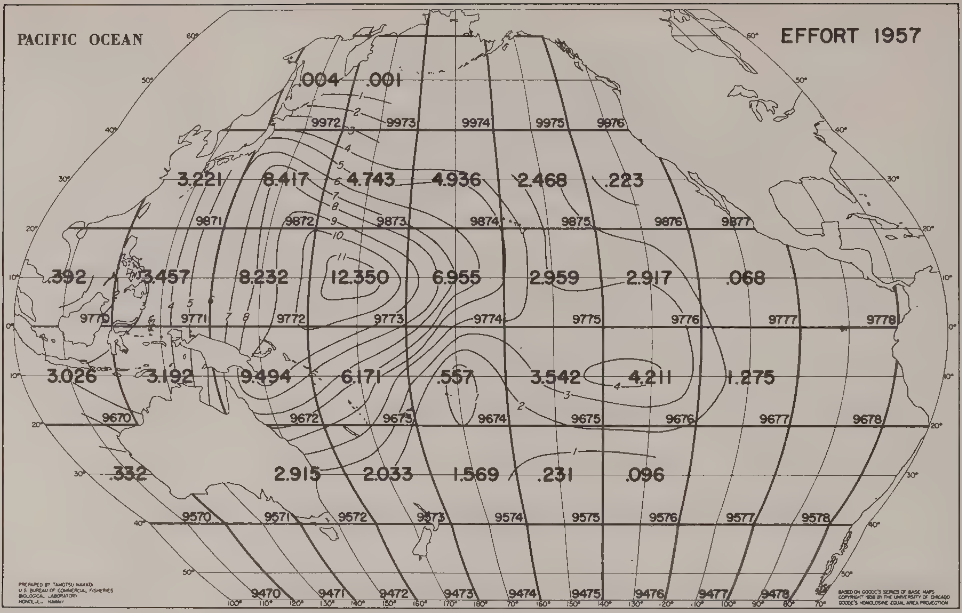
PACIFIC OCEAN
EFFORT 1957
.004
.001
9972
9973
9974
9975
9976
3.221
8.417
4.743
4.936
2.468
.223
9871
9872
9873
9874
9875
9876
9877
.392
3.457
8.232
12.350
6.955
2.959
2.917
.068
9770
9771
9772
9773
9774
9775
9776
9777
9778
3.026
3.192
9.494
6.171
.557
3.542
4.211
1.275
9670
9672
9673
9674
9675
9676
9677
9678
.332
2.915
2.033
1.569
.231
.096
9570
9571
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Figure 6e.--Percentage of reported total annual effort (numbers of hooks) expended in each 20-degree quadrangle in 1957.

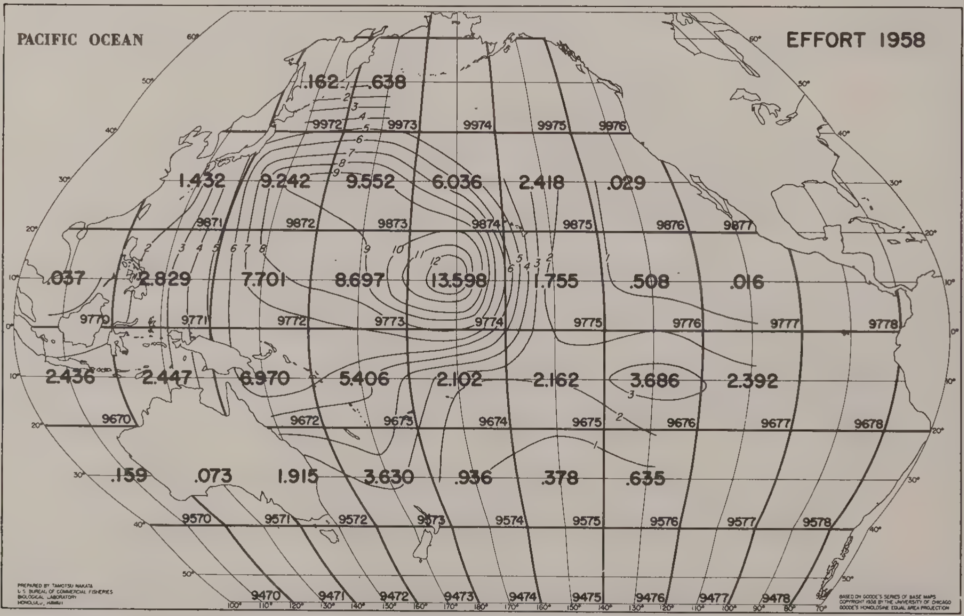
PACIFIC OCEAN
EFFORT 1958
.162
.638
9972
9973
9974
9975
9976
1.432
9.242
9.552
6.036
2.418
.029
9871
9872
9873
9874
9875
9876
9877
.037
2.829
7.701
8.697
13.598
1.755
.508
.016
9770
9771
9772
9773
9774
9775
9776
9777
9778
2.436
2.447
6.970
5.406
2.102
2.162
3.686
2.392
9670
9672
9673
9674
9675
9676
9677
9678
.159
.073
1.915
3.630
.936
.378
.635
9570
9571
9572
9573
9574
9575
9576
9577
9578
9470
9471
9472
9473
9474
9475
9476
9477
9478
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Figure 6f.--Percentage of reported total annual effort (numbers of hooks) expended in each 20-degree quadrangle in 1958.

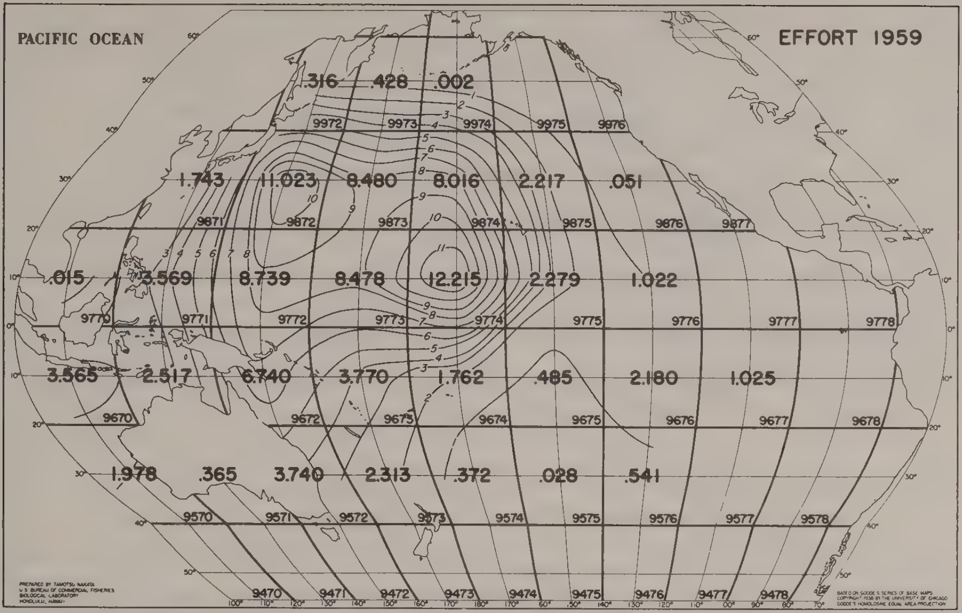
PACIFIC OCEAN
EFFORT 1959
.316
.428
.002
9972
9973
9974
9975
9976
1.743
11.023
8.480
8.016
2.217
.051
9871
9872
9873
9874
9875
9876
9877
.015
3.569
8.739
8.478
12.215
2.279
1.022
9770
9771
9772
9773
9774
9775
9776
9777
9778
3.565
2.517
6.740
3.770
1.762
.485
2.180
1.025
9670
9672
9673
9674
9675
9676
9677
9678
1.978
.365
3.740
2.313
.372
.028
.541
9570
9571
9572
9573
9574
9575
9576
9577
9578
9470
9471
9472
9473
9474
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Figure 6g.--Percentage of reported total annual effort (numbers of hooks) expended in each 20-degree quadrangle in 1959.

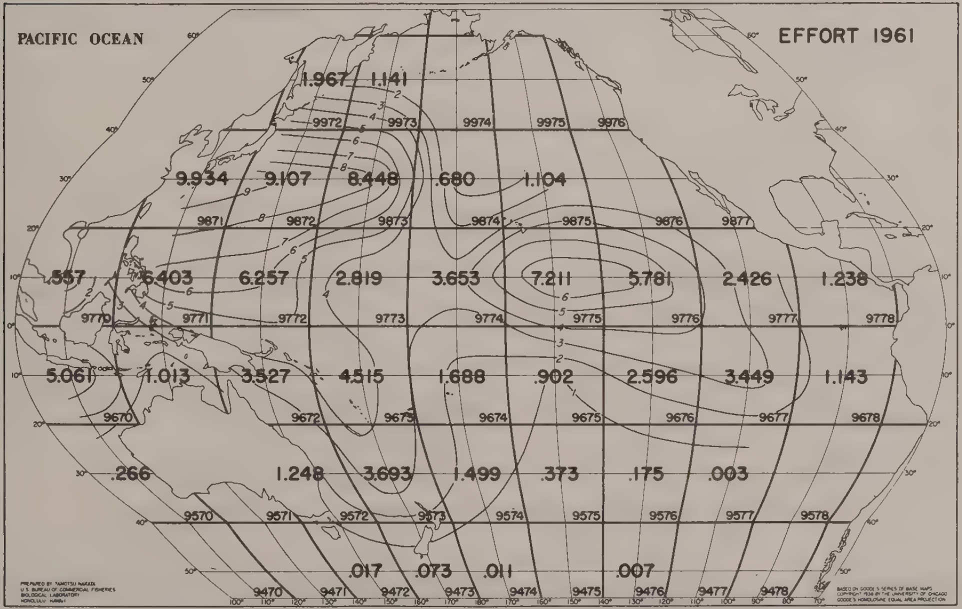
PACIFIC OCEAN
EFFORT 1961
1.967
1.141
9972
9973
9974
9975
9976
9.934
9.107
8.448
.680
1.104
9871
9872
9873
9874
9875
9876
9877
.557
6.403
6.257
2.819
3.653
7.211
5.781
2.426
1.238
9770
9771
9772
9773
9774
9775
9776
9777
9778
5.061
1.013
3.527
4.515
1.688
.902
2.596
3.449
1.143
9670
9672
9673
9674
9675
9676
9677
9678
.266
1.248
3.693
1.499
.373
.175
.003
9570
9571
9572
9573
9574
9575
9576
9577
9578
.017
.073
.011
.007
9470
9471
9472
9473
9474
9475
9476
9477
9478
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Figure 6h.--Percentage of reported total annual effort (numbers of hooks) expended in each 20-degree quadrangle in 1961.

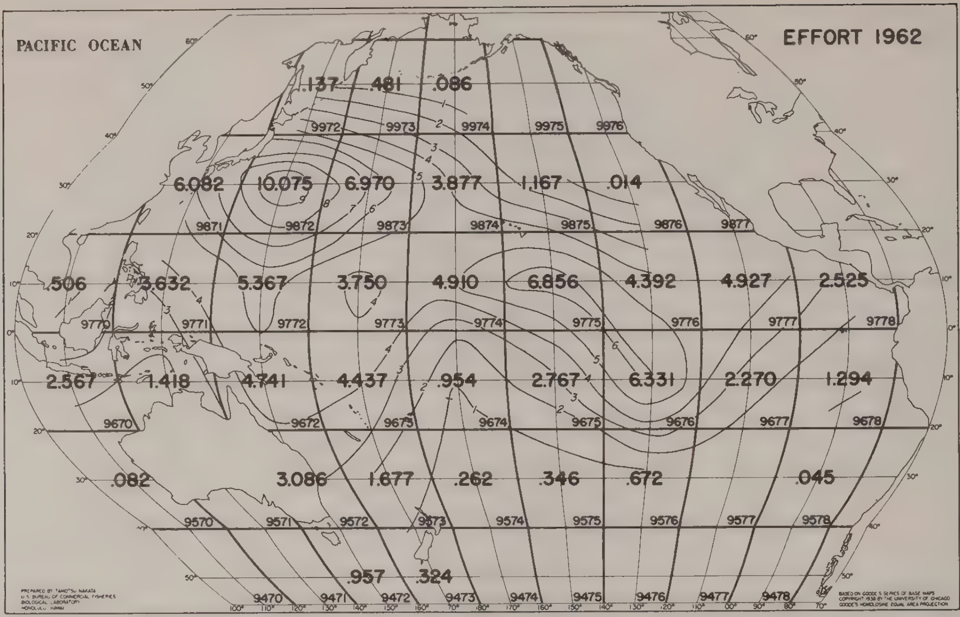
PACIFIC OCEAN
EFFORT 1962
.137
.481
.086
6.082
10.075
6.970
3.877
1.167
.014
.506
3.632
5.367
3.750
4.910
6.856
4.392
4.927
2.525
2.567
1.418
4.741
4.437
.954
2.767
6.331
2.270
1.294
.082
3.086
1.677
.262
.346
.672
.045
.957
.324

Figure 6i.--Percentage of reported total annual effort (numbers of hooks) expended in each 20-degree quadrangle in 1962.

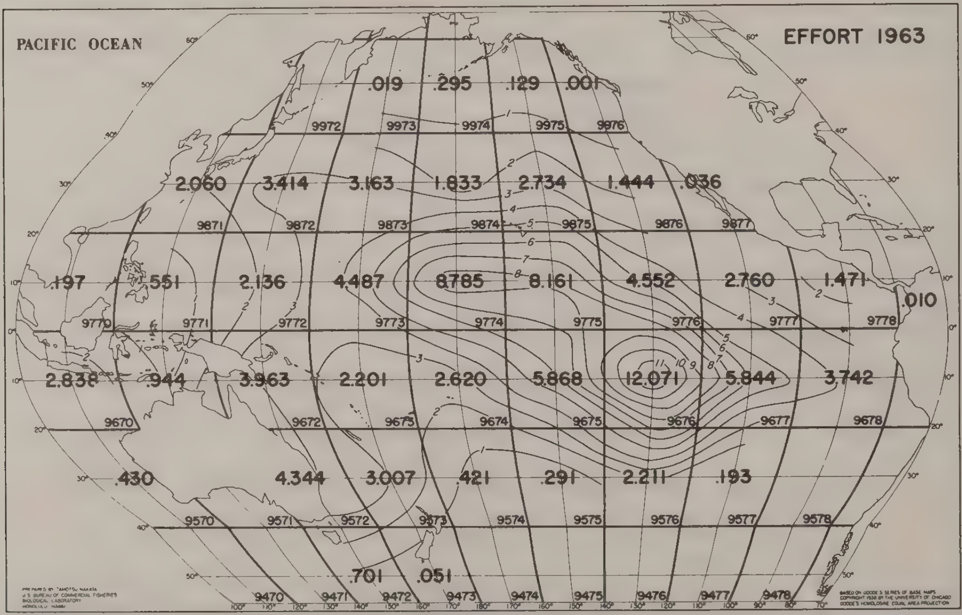
PACIFIC OCEAN
EFFORT 1963
.019
.295
.129
.001
2.060
3.414
3.163
1.833
2.734
1.444
.036
.197
.551
2.136
4.487
8.785
8.161
4.552
2.760
1.471
.010
2.838
.944
3.963
2.201
2.620
5.868
12.071
5.844
3.742
.430
4.344
3.007
.421
.291
2.211
.193
.701
.051

Figure 6j.--Percentage of reported total annual effort (numbers of hooks) expended in each 20-degree quadrangle in 1963.

contour interval indicates a degree of resolution beyond that which can be expected from 20-degree quadrangles.

Major concentrations of reported effort were expended just east of the Japanese archipelago in the vicinity of quadrangle 9872 in nearly all years. Two other trends in concentration of effort are evident. In the earlier years effort tended to be concentrated in the New Guinea-Solomon Islands region, in the vicinity of quadrangle 9672. A more dramatic trend, however, is the eastward movement of reported effort with time. This movement is evident not only in increased numbers of 20-degree quadrangles fished each year, but also in the location of effort concentrations. The first concentration east of quadrangle 9872 was in quadrangle 9774 in 1955. In 1957 a concentration of effort appeared in quadrangle 9775, and in 1963 in 9676. In 1956-62 the areas of concentration were essentially bimodal, consisting of a concentration near Japan and one in "distant waters" to the east.

Effort was initially concentrated, then, near the Japanese fishing ports. A later tendency to expand effort concentration to the south was overshadowed by expansion to the east. Despite the expansion to the east, a large proportion of each year's effort continued to be expended in the western Pacific until 1963, when the dominant concentration of effort appeared in the southeastern Pacific.

DISTRIBUTION OF CATCH

The distribution of catch in terms of the reported numbers of each species caught by location and year is also considered in terms of zonal percentages of annual catch.

The longitudinal zonal percentages for yellowfin tuna (fig. 7), show that the percentage caught in each zone tends to parallel the longitudinal zonal percentages of the hooks set in each zone. By contrast, the peak concentrations of bigeye tuna catches (fig. 8) tend to be located east of the major concentrations of effort. In the most recent years, 1961-63, the greatest proportion of the yellowfin tuna catch was taken from the area of the Pacific which lies west of the longitude of Hawaii, whereas the

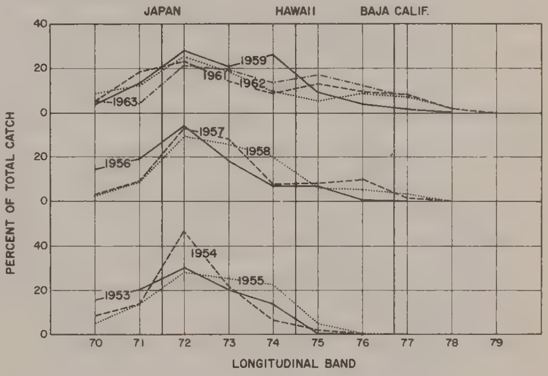

Figure 7.--Percentage of reported total annual catch (numbers of fish) of yellowfin tuna taken in each longitudal band in 1953-63.

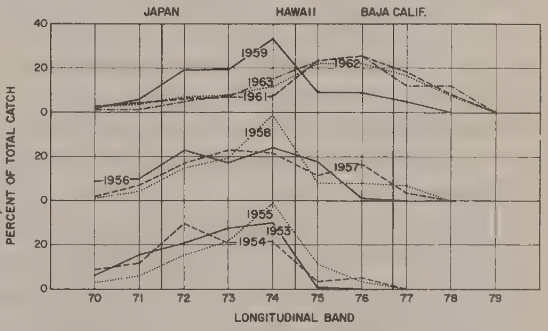

Figure 8.--Percentage of reported total annual catch (numbers of fish) of bigeye tuna taken in each longitudinal band in 1953-63.

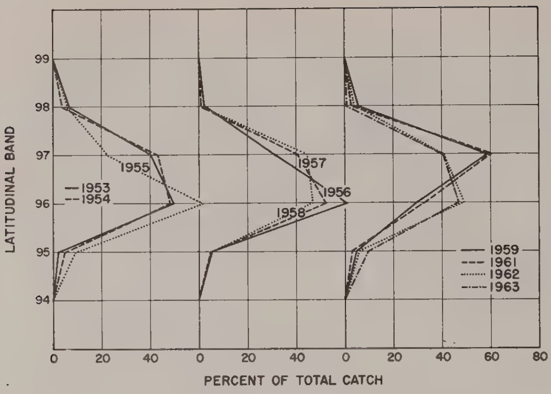

Figure 9.--Percentage of reported total annual catch (numbers of fish) of yellowfin tuna taken in each latitudinal band in 1953-63.

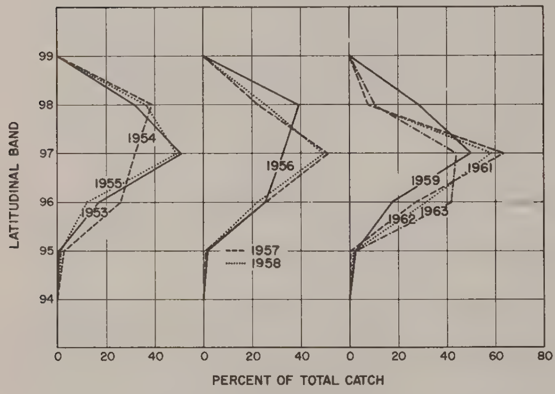

Figure 10.--Percentage of reported total annual catch (numbers of fish) of bigeye tuna taken in each latitudinal band in 1953-63.

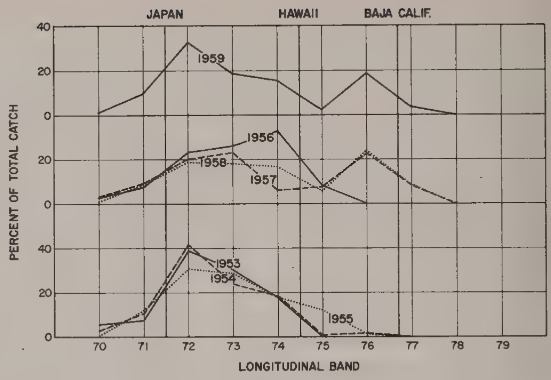

Figure 11.--Percentage of reported total annual catch (numbers of fish) of skipjack tuna taken in each longitudinal band in 1953-59.

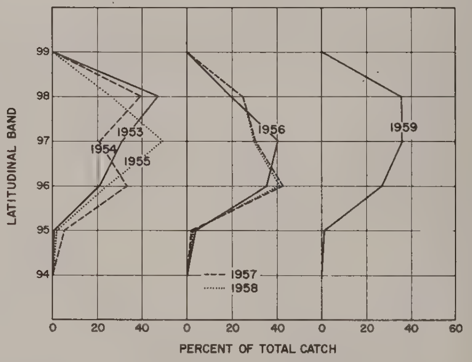

Figure 12.--Percentage of reported total annual catch (numbers of fish) of skipjack tuna taken in each latitudinal band in 1953-59.

greatest proportion of the bigeye tuna catch was taken from the area east of this longitude.

The latitudinal zonal distribution of yellowfin tuna catch (fig. 9) shows that peak concentrations were in the Southern Hemisphere for all years except 1959 and 1961. The latitudinal zonal distribution of the catch of bigeye tuna (fig. 10) shows modal values in latitudinal band 98 in 1954 and 1956, and in band 97 in all other years; in 1963, however, the percentage caught in band 96 nearly equaled the percentage caught in band 97.

The skipjack tuna is one of the fishes taken least commonly on longline gear. Data on skipjack tuna catches are given in Tuna Fishing only until 1959. The degree to which the recorded data on skipjack tuna represent the actual

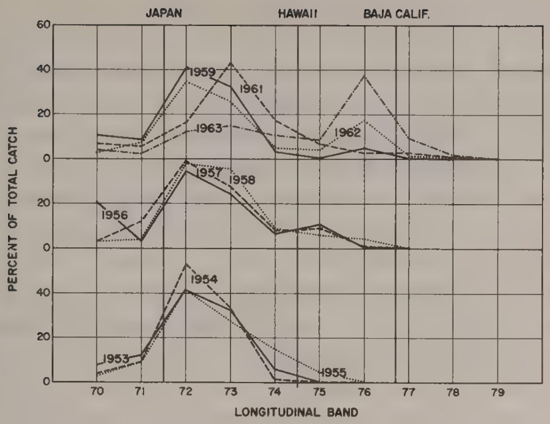

Figure 13.--Percentage of reported total annual catch (numbers of fish) of albacore taken in each longitudinal band in 1953-63.

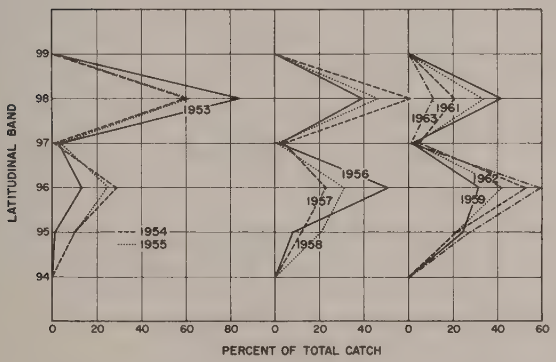

Figure 14.--Percentage of reported total annual catch (numbers of fish) of albacore taken in each latitudinal band in 1953-63.

catches taken by the longline fleet is not certain; nevertheless, the data are presented for completeness. The longitudinal zonal distribution of skipjack tuna catches (fig. 11) for 1953-59 approximates the distribution of effort. Relatively higher catches of skipjack tuna are apparent in band 76 in 1956-59 than in earlier years. No strong trends are discernible in the latitudinal zonal percentages of skipjack tuna (fig. 12).

Although the major emphasis of this paper is on the yellowfin, bigeye, and skipjack tunas, the distribution of albacore catches is considered briefly, since this species may be caught in conjunction with the other three species. The zonal percentages of the number of albacore caught each year are given in figures 13 and 14. A striking feature of these figures is the higher degree of concentration of catches of albacore than of the other species of tunas. Peak catches were in longitudinal band 72 in 1953-59 and in band 73 in 1961, reverted to band 72 in 1962, and jumped to band 76 in 1963. The percentage of albacore caught in the eastern Pacific increased with time; high percentages are particularly apparent in band 76 in 1962 and 1963. The latitudinal zonal percentages show a clear bimodality in distribution; peak concentrations are in bands 98 and 96 and the species is practically absent in band 97. In the early years, 1953-55, most albacore were caught in the North Pacific, but in 1961-63 most were taken in the South Pacific Ocean. Detailed studies on the dynamics of the albacore fishery in the South Pacific are being made by Otsu and Sumida (MS.)[1] and Otsu (1966).

The distribution of catch, then, shows that the majority of yellowfin tuna are taken in the southwestern Pacific and the majority of bigeye tuna in waters east of the Hawaiian Islands. Albacore are caught in the North and South Pacific; initially the major catches of albacore were from the northwest Pacific Ocean, but a trend toward the east and the south, similar to the trend in the distribution of bigeye tuna catches, is evident. It seems clear that the eastward extension of effort is associated with the extensive catches of bigeye tuna (and possibly albacore, to a lesser extent) which have been made in the area east of the Hawaiian Islands.

---

[1] Otsu, T., and R. F. Sumida. MS. Distribution, apparent abundance, and size composition of albacore (Thunnus alalunga) taken in the Samoa-based longline fishery, 1964-65. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii.

APPARENT ABUNDANCE

The temporal-spatial distribution of apparent abundance (measured by the CPUE, which in this paper is defined as the ratio of average catch to average effort for a particular time-space unit) of yellowfin, bigeye, and skipjack tunas are considered in this section. The discussions of apparent abundance concentrates on CPUE for yellowfin and bigeye tunas for each year and 20-degree quad-

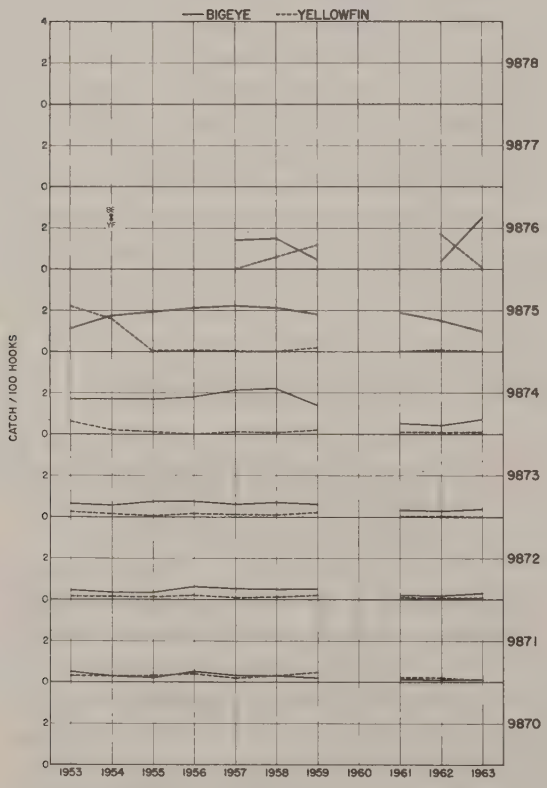

Figure 15a.--Annual catch per 100 hooks for bigeye and yellowfin tunas for each 20-degree quadrangle in latitudinal band 98.

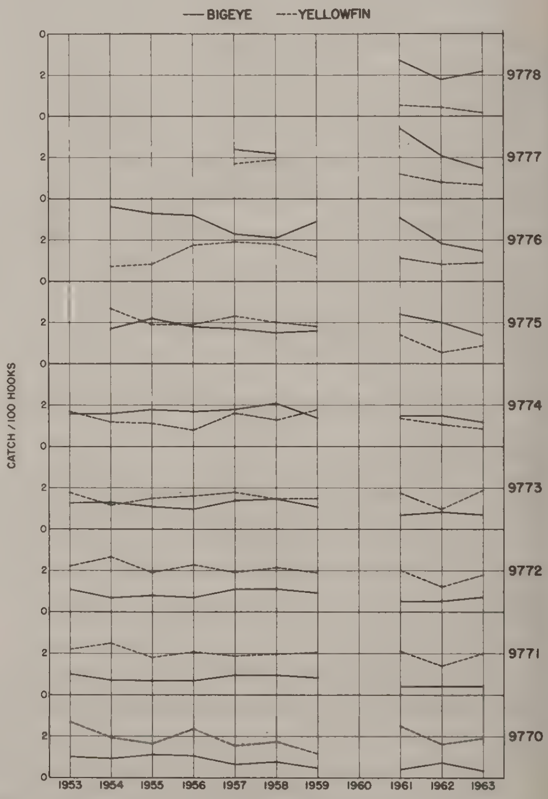

Figure 15b.--Annual catch per 100 hooks for bigeye and yellowfin tunas for each 20-degree quadrangle in latitudinal band 97.

rangle; deviations in CPUE, for each 20-degree quadrangle, from the CPUE for the entire Pacific for each year for bigeye, yellowfin, and skipjack tunas; and finally, monthly CPUE data on yellowfin and bigeye tunas for selected 20-degree quadrangles in the vicinity of the Hawaiian Islands.

Catch Per Unit of Effort (CPUE) by Years and 20-Degree Quadrangles

The CPUE's for bigeye and yellowfin tunas for each year and 20-degree quadrangle are grouped by latitudinal bands in figure 15.

The CPUE for yellowfin tuna was at a relatively low level throughout the northernmost band, 98 (fig. 15a); the CPUE for bigeye tuna was also relatively low except for the vicinity of the Hawaiian Islands, in quadrangles 9874 and 9875, where relatively high indices of abundance are attained. The most evident temporal change in band 98 is the decline, after 1958, in apparent abundance of bigeye tuna in quadrangles 9874 and 9875. A sharp decline in CPUE for yellowfin tuna is also evident after 1954 in quadrangle 9875.

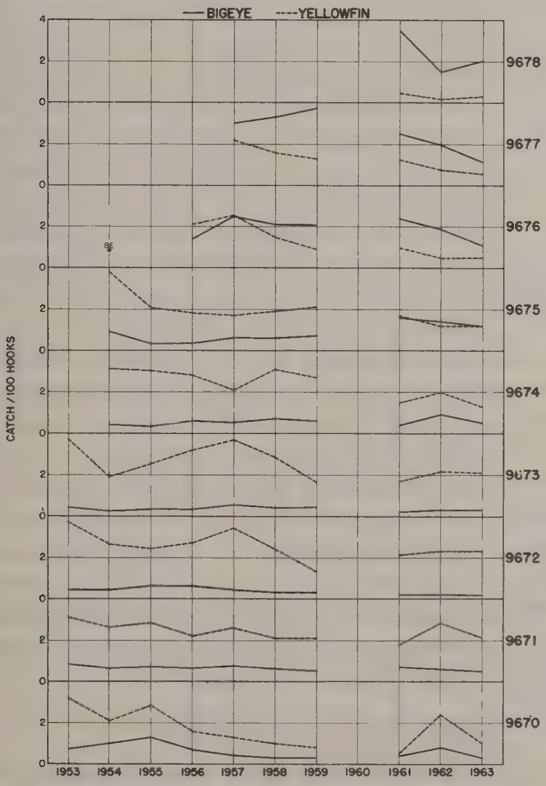

Figure 15c.--Annual catch per 100 hooks for bigeye and yellowfin tunas for each 20-degree quadrangle in latitudinal band 96.

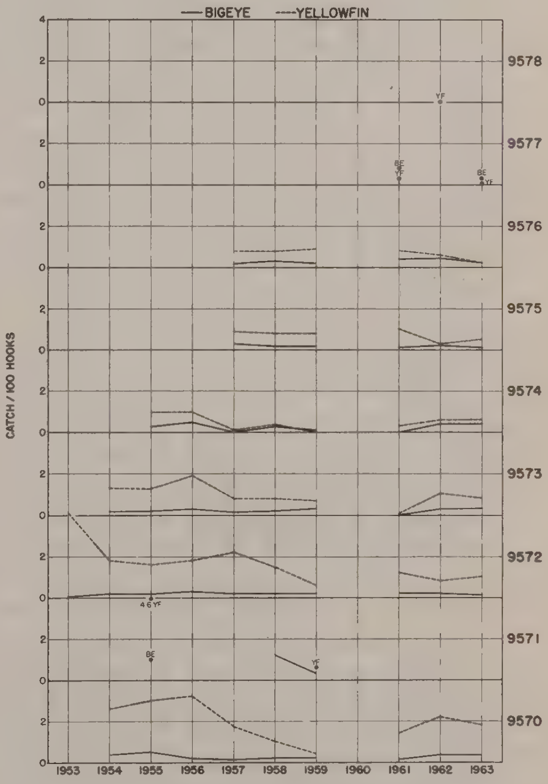

Figure 15d.--Annual catch per 100 hooks for bigeye and yellowfin tunas for each 20-degree quadrangle in latitudinal band 95.

Band 97, just south of the northernmost band, occupies the region between 0° and lat. 20° N. Here both the bigeye and yellowfin tunas are--with the exception of the bigeye tuna in quadrangles 9874 and 9875--at noticeably higher levels of apparent abundance than in band 98. Yellowfin tuna appear to be most abundant in the western portion of the band, but bigeye tuna are more abundant in the eastern portion. The location of transition in predominant apparent abundance, from yellowfin tuna to bigeye tuna, in band 97 is in quadrangles 9774 or 9775 at the longitude of the Hawaiian Islands. With respect to temporal changes in apparent abundance, CPUE for the yellowfin tuna in the western Pacific is about the same in the 1961-63 and 1953-59 periods or is higher in the post-1960 period. In the eastern Pacific, however, the CPUE of yellowfin tuna appears to be less in the post-1960 period than in the pre-1960 period. The CPUE for bigeye tuna appears to decline after 1958 in quadrangles 9770 through 9774. East of 9774, a decline is also evident, but begins in 1961 rather than in 1958.

Latitudinal band 96 is the 20-degree strip from the Equator southward. This band is similar to 97 in the sense that the apparent abundance of yellowfin tuna is greater than that of bigeye tuna in the western regions of the band but not in the eastern. In band 96, however, the difference between apparent abundance of yellowfin and bigeye tunas is relatively much greater than that in band 97. Also, the transition in greater apparent abundance, from yellowfin tuna to bigeye tuna, occurs farther east in band 96 than in band 97. With respect to temporal trends in band 96, the CPUE of yellowfin tuna is much more variable than the same statistics in band 97. West of quadrangle 9674, the CPUE of yellowfin tuna appears to be greater, on the average, in the post-1960 period than in the late 1950's; the CPUE for the post-1960 period is also less than that of the early 1950's. In quadrangles east of 9674 many year-to-year decreases in the apparent abundance of yellowfin tuna are apparent. Temporal changes in the CPUE of bigeye tuna are not particularly evident in the western portion of band 96. In quadrangle 9675 bigeye tuna CPUE appears to increase in the post-1960 period over the pre-1960 period. Almost consistent decreases in the CPUE of bigeye tuna are evident in the post-1960 period in the region east of quadrangle 9675.

The southernmost band, 95, occupies the latitudinal strip between 20° and 40° S. Relatively high CPUE's for yellowfin tuna are also evident in the western portion of this band. As in the other bands, the apparent abundance of yellowfin tuna declines from west to east. The apparent abundance of bigeye tuna does not, however, increase to the east as in the other bands; this may be an artifact of the relatively limited eastward extension of fishing effort in band 95. The dominant temporal trend in band 95 is the average decrease in CPUE of yellowfin tuna with time. The levels of apparent abundance of yellowfin tuna tend to be higher in the beginning of the post-1960 period than in 1959. There are no striking temporal trends in the CPUE for bigeye tuna.

Deviations from Annual CPUE

The preceding section emphasized temporal changes in CPUE for each quadrangle. The present section, with the same data, emphasizes the spatial variation for each year, species, and

20-degree quadrangle. The spatial variation is presented in terms of the deviation of CPUE of each species, year, and quadrangle from the average CPUE of each species and year for the entire Pacific Ocean. These deviations, which must, of course, be regarded only as indices, are given in figures 16, 17, and 18 for bigeye, yellowfin, and skipjack tunas. The positive deviations are unshaded, the negative deviations shaded. The unshaded regions show those locations where ''above average'' indices of abundance were obtained for the various species in each year.

For the bigeye tuna (fig. 16) positive deviations persist in the eastern Pacific and negative deviations in the western Pacific. The north equatorial band (97) exhibits the westernmost extension of positive deviations. The center of the positive deviations is initially in the north central Pacific, moves eastward in intermediate years, and eventually extends into the southeastern Pacific.

For the yellowfin tuna (fig. 17) most of the negative deviations in CPUE before 1956 are in the quadrangles north of lat. 20° N. As the fishery extended south of lat. 20° S., negative deviations also appear in this region. Until 1961, the highest apparent abundance of yellowfin tuna was in the 20-degree bands north and south of the Equator. In 1962 and 1963, however, negative deviations appear in the eastern Pacific. Positive deviations in recent years are in the western (particularly southwestern) equatorial Pacific.

For the skipjack tuna (fig. 18) the deviations, as well as the CPUE's, are small. It is possible that a large component of variation in CPUE is random. In 1953, positive deviations were in the northwest Pacific, west of the Philippines, and along the easternmost perimeter of the fished area. In 1954-56 most of the positive deviations were in the western portion of the north equatorial band and in the south equatorial band; the positive deviations in the north equatorial band, however, tended to lie east of the positive deviations in the south equatorial band.

Positive deviations in CPUE for skipjack tuna continue to appear in the eastern portion of the fishery area in 1957-59, and are again present off the Japanese archipelago. Notably, the maximum positive deviation for skipjack tuna is always in the South Pacific (band 96), in the vicinity of the eastern extension of the fishery, and this maximum deviation tends to be substantially larger than most positive deviations for skipjack tuna in that period.

Kawasaki (1964), who examined longline data pooled for 1956-60 in the region between lat. 15° and 40° N. and extending from the Japanese coast to long. 150° W., showed that peak apparent abundance of skipjack tuna in the winter longline fishery is in January and February. The skipjack tuna taken by this fishery are likely to be large fish (>60 cm.). The possible correlation between the appearance of large fish in midwinter in both the Japanese longline fishery and the Hawaiian pole-and-line fishery is worth further examination.

Monthly CPUE Data

Summarization of catch, effort, and CPUE in terms of annual averages tends to mask apparently periodic variability in these data. Some of the variability is demonstrated in the monthly CPUE data of bigeye and yellowfin tunas for the four 20-degree quadrangles (9874, 9875, 9774, and 9775) whose boundaries inter-

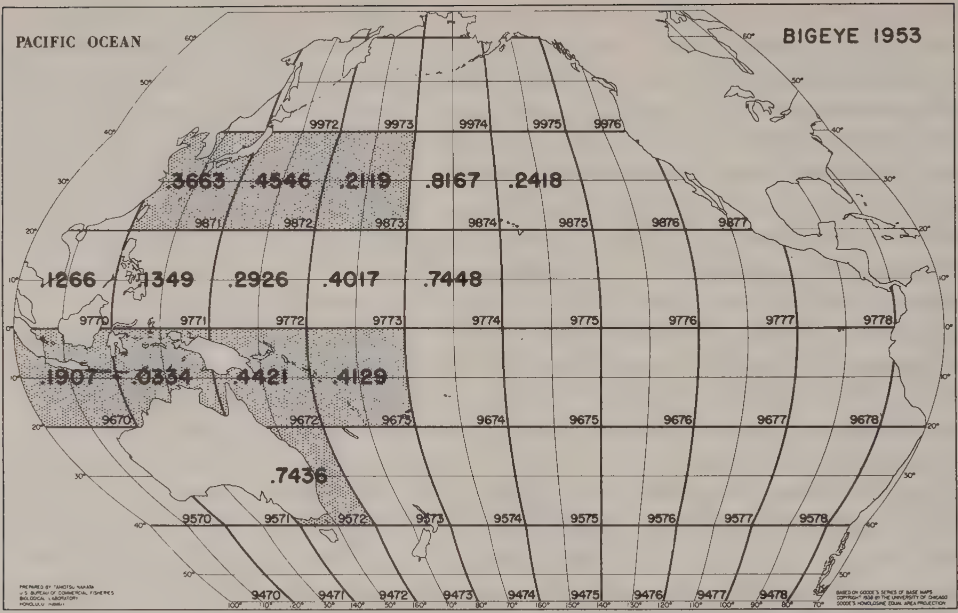
PACIFIC OCEAN
BIGEYE 1953
9972 9973 9974 9975 9976
.3663 .4546 .2119 .8167 .2418
9871 9872 9873 9874 9875 9876 9877
.1266 .1349 .2926 .4017 .7448
9770 9771 9772 9773 9774 9775 9776 9777 9778
.1907 .0334 .4421 .4129
9670 9672 9673 9674 9675 9676 9677 9678
.7436
9570 9571 9572 9573 9574 9575 9576 9577 9578
9470 9471 9472 9473 9474 9475 9476 9477 9478
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Figure 16a.--Bigeye tuna, 1953: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

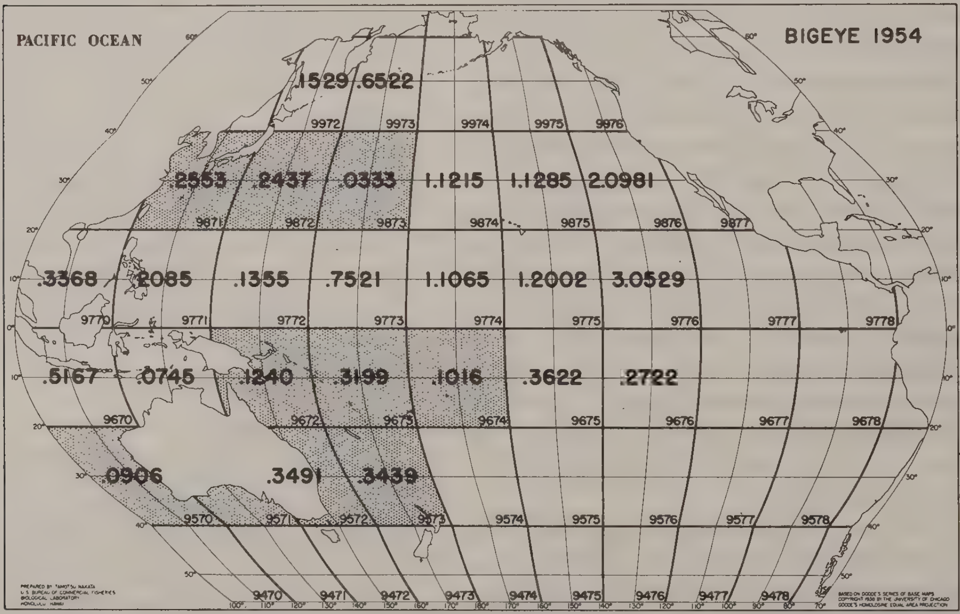
PACIFIC OCEAN
BIGEYE 1954
.1529 .6522
9972 9973 9974 9975 9976
.2553 .2437 .0333 1.1215 1.1285 2.0981
9871 9872 9873 9874 9875 9876 9877
.3368 .2085 .1355 .7521 1.1065 1.2002 3.0529
9770 9771 9772 9773 9774 9775 9776 9777 9778
.5167 .0745 .1240 .3199 .1016 .3622 .2722
9670 9672 9673 9674 9675 9676 9677 9678
.0906 .3491 .3439
9570 9571 9572 9573 9574 9575 9576 9577 9578
9470 9471 9472 9473 9474 9475 9476 9477 9478
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Figure 16b.--Bigeye tuna, 1954: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

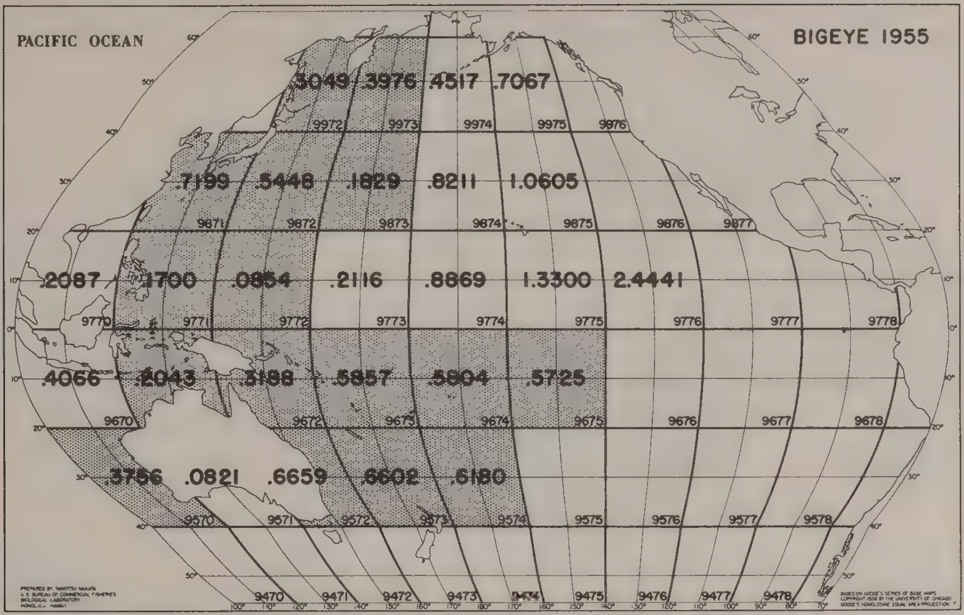
PACIFIC OCEAN
BIGEYE 1955
.3049 .3976 .4517 .7067
9972 9973 9974 9975 9976
.7199 .5448 .1829 .8211 1.0605
9871 9872 9873 9874 9875 9876 9877
.2087 .1700 .0854 .2116 .8869 1.3300 2.4441
9770 9771 9772 9773 9774 9775 9776 9777 9778
.4066 .2043 .3188 .5857 .5804 .5725
9670 9672 9673 9674 9675 9676 9677 9678
.3756 .0821 .6659 .6602 .6180
9570 9571 9572 9573 9574 9575 9576 9577 9578
9470 9471 9472 9473 9474 9475 9476 9477 9478
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Figure 16c.--Bigeye tuna, 1955: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

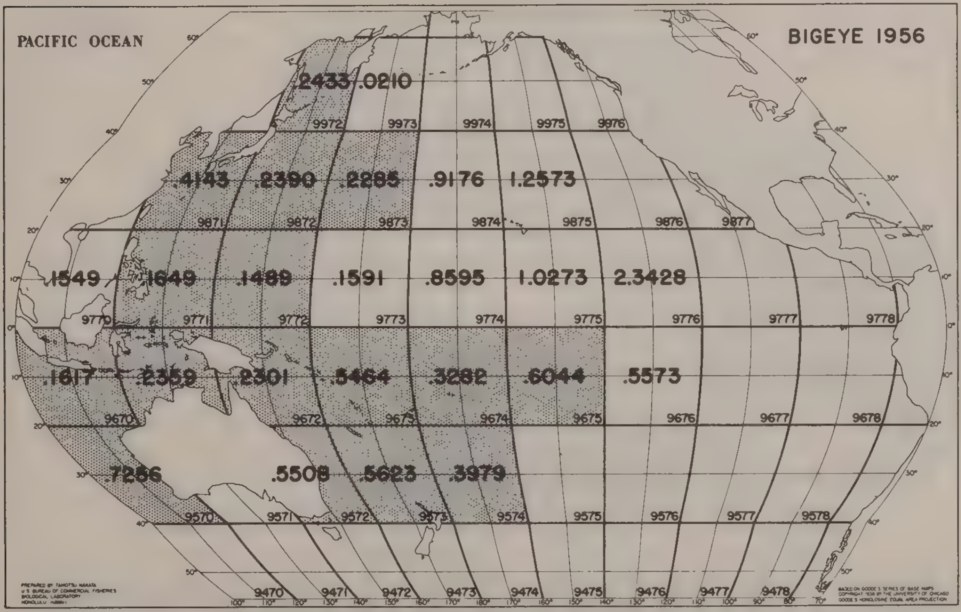
PACIFIC OCEAN
BIGEYE 1956
.2433 .0210
9972 9973 9974 9975 9976
.4143 .2390 .2285 .9176 1.2573
9871 9872 9873 9874 9875 9876 9877
.1549 .1649 .1489 .1591 .8595 1.0273 2.3428
9770 9771 9772 9773 9774 9775 9776 9777 9778
.1617 .2359 .2301 .5464 .3282 .6044 .5573
9670 9672 9673 9674 9675 9676 9677 9678
.7266 .5508 .5623 .3979
9570 9571 9572 9573 9574 9575 9576 9577 9578
9470 9471 9472 9473 9474 9475 9476 9477 9478
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Figure 16d.--Bigeye tuna, 1956: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

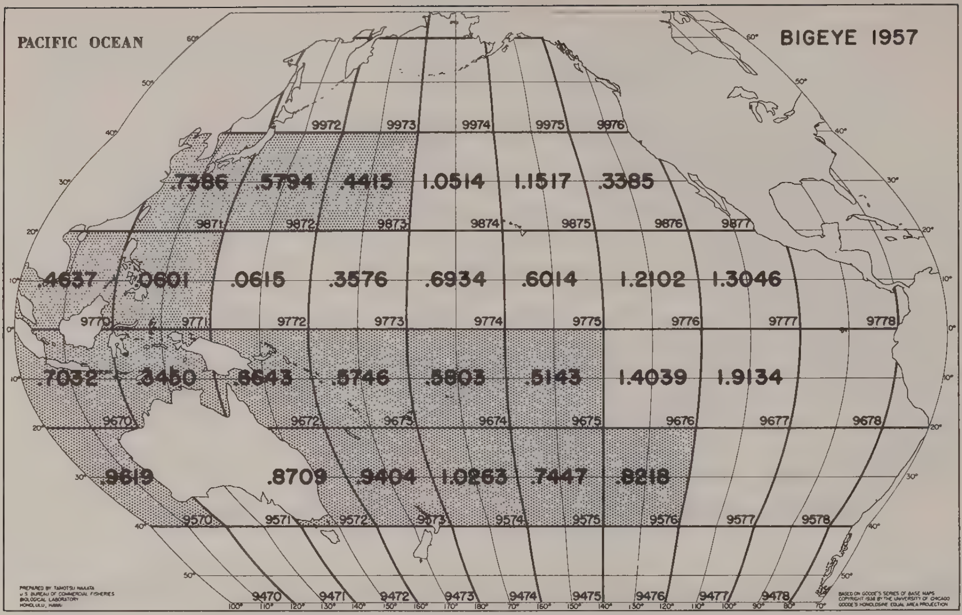
PACIFIC OCEAN
BIGEYE 1957
9972 9973 9974 9975 9976
.7386 .5794 .4415 1.0514 1.1517 .3385
9871 9872 9873 9874 9875 9876 9877
.4637 .0601 .0615 .3576 .6934 .6014 1.2102 1.3046
9770 9771 9772 9773 9774 9775 9776 9777 9778
.7032 .3450 .8643 .5746 .5803 .5143 1.4039 1.9134
9670 9672 9673 9674 9675 9676 9677 9678
.9619 .8709 .9404 1.0263 .7447 .8218
9570 9571 9572 9573 9574 9575 9576 9577 9578
9470 9471 9472 9473 9474 9475 9476 9477 9478
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Figure 16e.--Bigeye tuna, 1957: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

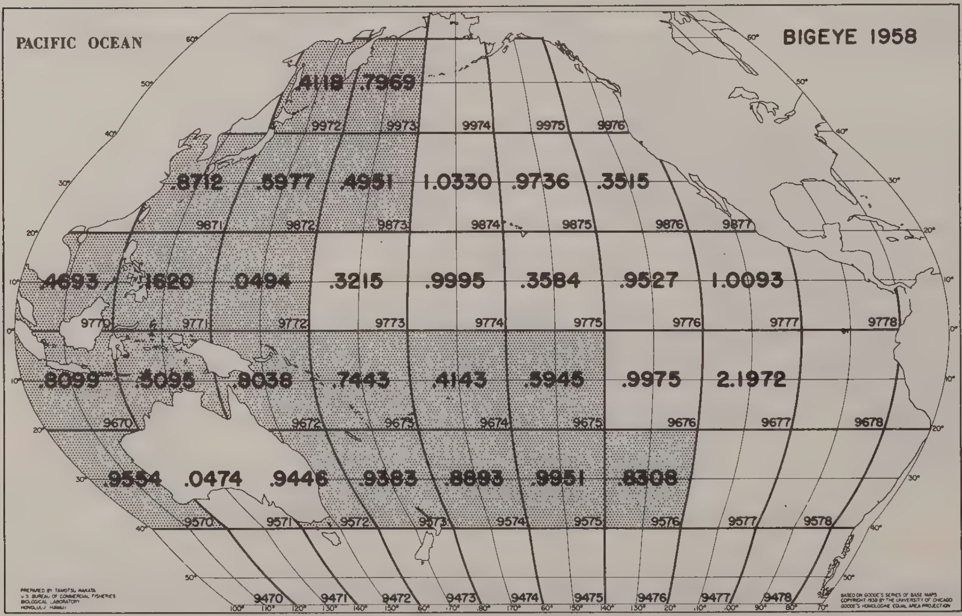
PACIFIC OCEAN
BIGEYE 1958
.4118 .7969
9972 9973 9974 9975 9976
.8712 .5977 .4951 1.0330 .9736 .3515
9871 9872 9873 9874 9875 9876 9877
.4693 .1620 .0494 .3215 .9995 .3584 .9527 1.0093
9770 9771 9772 9773 9774 9775 9776 9777 9778
.8099 .5095 .8038 .7443 .4143 .5945 .9975 2.1972
9670 9672 9673 9674 9675 9676 9677 9678
.9554 .0474 .9446 .9383 .8893 .9951 .8308
9570 9571 9572 9573 9574 9575 9576 9577 9578
9470 9471 9472 9473 9474 9475 9476 9477 9478
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Figure 16f.--Bigeye tuna, 1958: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

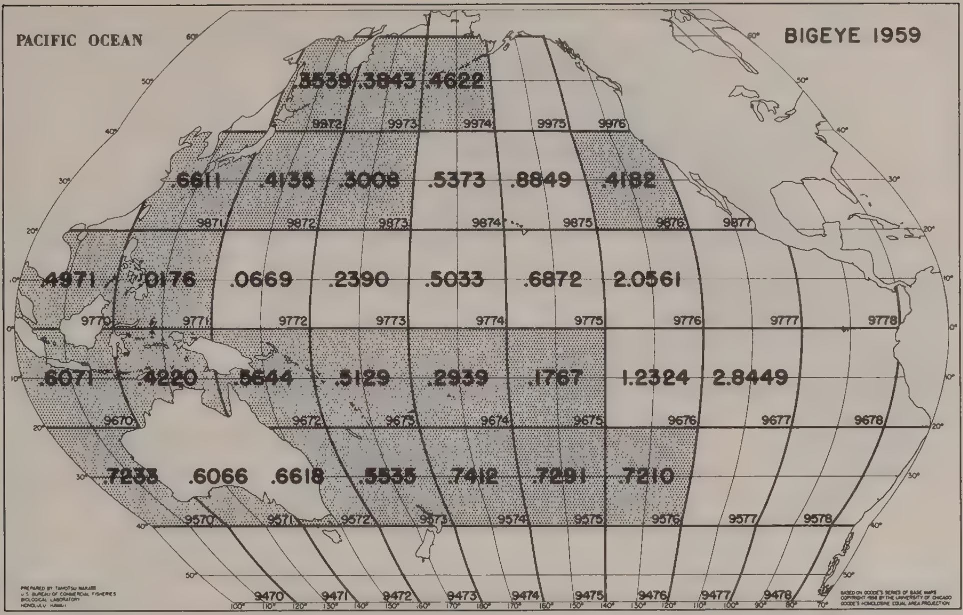
PACIFIC OCEAN
BIGEYE 1959
.3539
.3843
.4622
9972
9973
9974
9975
9976
.6611
.4135
.3008
.5373
.8849
.4182
9871
9872
9873
9874
9875
9876
9877
.4971
.0176
.0669
.2390
.5033
.6872
2.0561
9770
9771
9772
9773
9774
9775
9776
9777
9778
.6071
.4220
.5644
.5129
.2939
.1767
1.2324
2.8449
9670
9672
9673
9674
9675
9676
9677
9678
.7233
.6066
.6618
.5535
.7412
.7291
.7210
9570
9571
9572
9573
9574
9575
9576
9577
9578
9470
9471
9472
9473
9474
9475
9476
9477
9478
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Figure 16g.--Bigeye tuna, 1959: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

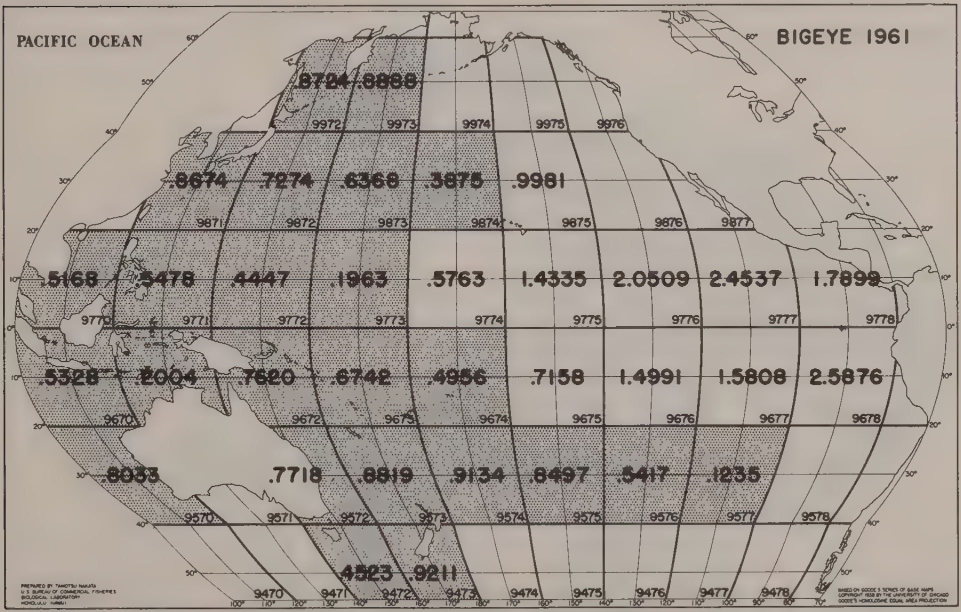
PACIFIC OCEAN
BIGEYE 1961
.8724
.8888
9972
9973
9974
9975
9976
.8674
.7274
.6368
.3875
.9981
9871
9872
9873
9874
9875
9876
9877
.5168
.5478
.4447
.1963
.5763
1.4335
2.0509
2.4537
1.7899
9770
9771
9772
9773
9774
9775
9776
9777
9778
.5328
.2004
.7620
.6742
.4956
.7158
1.4991
1.5808
2.5876
9670
9672
9673
9674
9675
9676
9677
9678
.8033
.7718
.8819
.9134
.8497
.5417
.1235
9570
9571
9572
9573
9574
9575
9576
9577
9578
.4523
.9211
9470
9471
9472
9473
9474
9475
9476
9477
9478
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Figure 16h.--Bigeye tuna, 1961: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

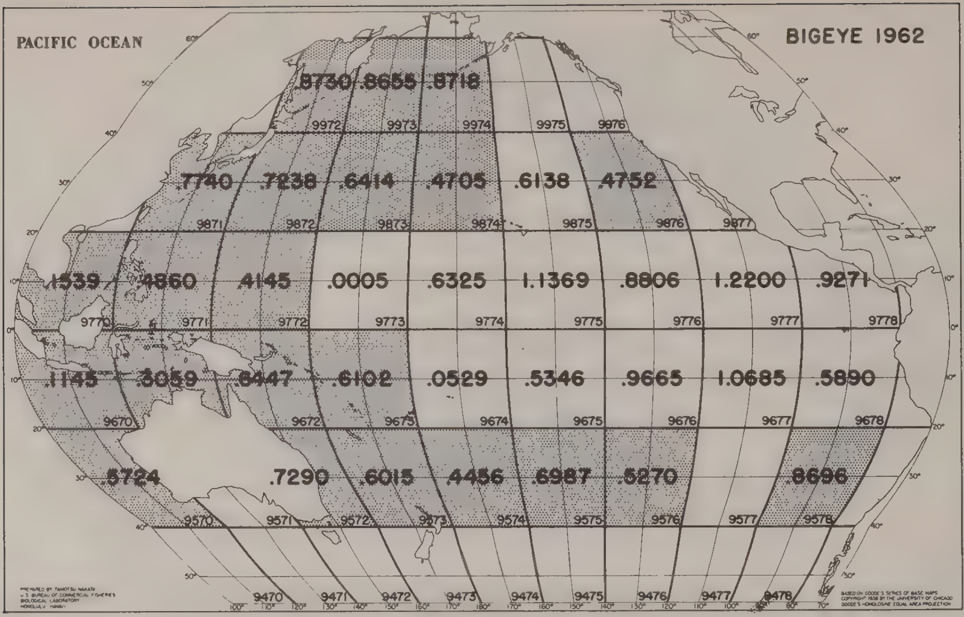
PACIFIC OCEAN
BIGEYE 1962
.8730 .8655 .8718
9972 9973 9974 9975 9976
.7740 .7238 .6414 .4705 .6138 .4752
9871 9872 9873 9874 9875 9876 9877
.1539 .4860 .4145 .0005 .6325 1.1369 .8806 1.2200 .9271
9770 9771 9772 9773 9774 9775 9776 9777 9778
.1145 .3059 .6447 .6102 .0529 .5346 .9665 1.0685 .5890
9670 9672 9673 9674 9675 9676 9677 9678
.5724 .7290 .6015 .4456 .6987 .5270 .8696
9570 9571 9572 9573 9574 9575 9576 9577 9578
9470 9471 9472 9473 9474 9475 9476 9477 9478

Figure 16i.--Bigeye tuna, 1962: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

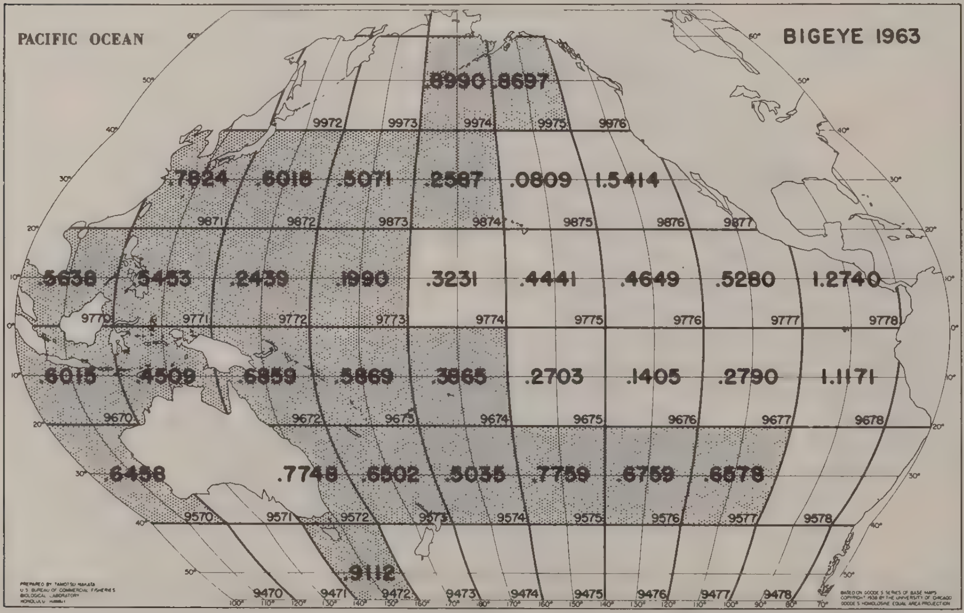
PACIFIC OCEAN
BIGEYE 1963
.8990 .8697
9972 9973 9974 9975 9976
.7824 .6018 .5071 .2587 .0809 1.5414
9871 9872 9873 9874 9875 9876 9877
.5638 .5453 .2439 .1990 .3231 .4441 .4649 .5280 1.2740
9770 9771 9772 9773 9774 9775 9776 9777 9778
.6015 .4509 .6859 .5869 .3865 .2703 .1405 .2790 1.1171
9670 9672 9673 9674 9675 9676 9677 9678
.6458 .7748 .6502 .5035 .7759 .6759 .6578
9570 9571 9572 9573 9574 9575 9576 9577 9578
.9112
9470 9471 9472 9473 9474 9475 9476 9477 9478

Figure 16j.--Bigeye tuna, 1963: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

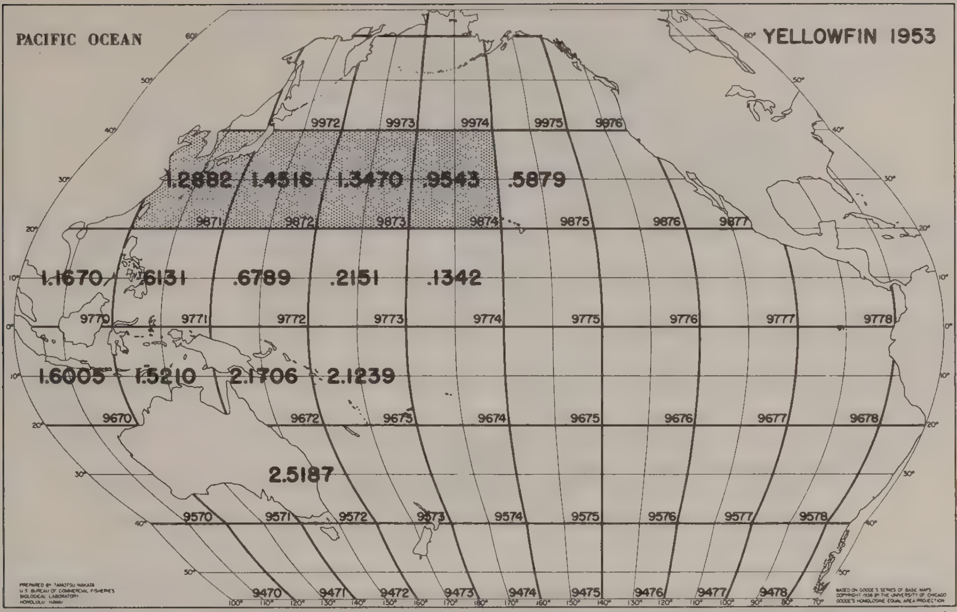
PACIFIC OCEAN
YELLOWFIN 1953
9972
9973
9974
9975
9976
1.2882
1.4516
1.3470
.9543
.5879
9871
9872
9873
9874
9875
9876
9877
1.1670
.6131
.6789
.2151
.1342
9770
9771
9772
9773
9774
9775
9776
9777
9778
1.6005
1.5210
2.1706
2.1239
9670
9672
9673
9674
9675
9676
9677
9678
2.5187
9570
9571
9572
9573
9574
9575
9576
9577
9578
9470
9471
9472
9473
9474
9475
9476
9477
9478

Figure 17a.--Yellowfin tuna, 1953: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

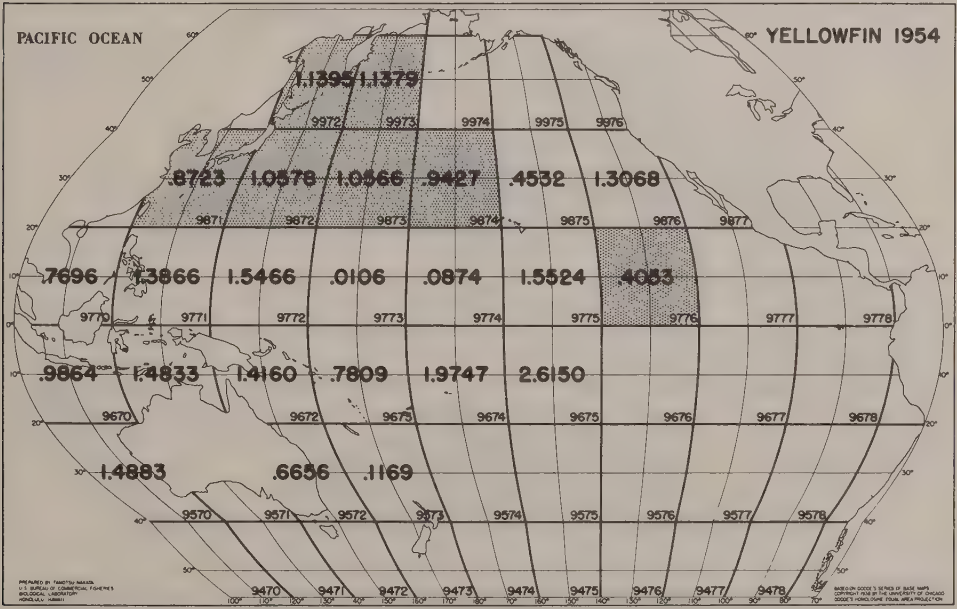
PACIFIC OCEAN
YELLOWFIN 1954
1.1395
1.1379
9972
9973
9974
9975
9976
.8723
1.0578
1.0566
.9427
.4532
1.3068
9871
9872
9873
9874
9875
9876
9877
.7696
1.3866
1.5466
.0106
.0874
1.5524
.4083
9770
9771
9772
9773
9774
9775
9776
9777
9778
.9864
1.4833
1.4160
.7809
1.9747
2.6150
9670
9672
9673
9674
9675
9676
9677
9678
1.4883
.6656
.1169
9570
9571
9572
9573
9574
9575
9576
9577
9578
9470
9471
9472
9473
9474
9475
9476
9477
9478

Figure 17b.--Yellowfin tuna, 1954: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

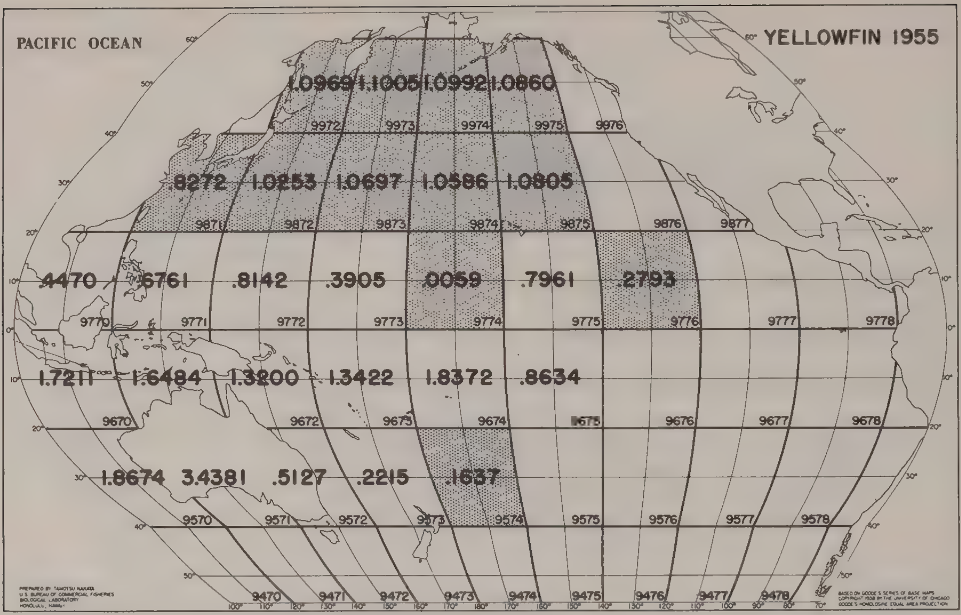
PACIFIC OCEAN
YELLOWFIN 1955
1.0969
1.1005
1.0992
1.0860
9972
9973
9974
9975
9976
.8272
1.0253
1.0697
1.0586
1.0805
9871
9872
9873
9874
9875
9876
9877
.4470
.6761
.8142
.3905
.0059
.7961
.2793
9770
9771
9772
9773
9774
9775
9776
9777
9778
1.7211
1.6484
1.3200
1.3422
1.8372
.8634
9670
9672
9673
9674
9675
9676
9677
9678
1.8674
3.4381
.5127
.2215
.1637
9570
9571
9572
9573
9574
9575
9576
9577
9578
9470
9471
9472
9473
9474
9475
9476
9477
9478
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Figure 17c.--Yellowfin tuna, 1955: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

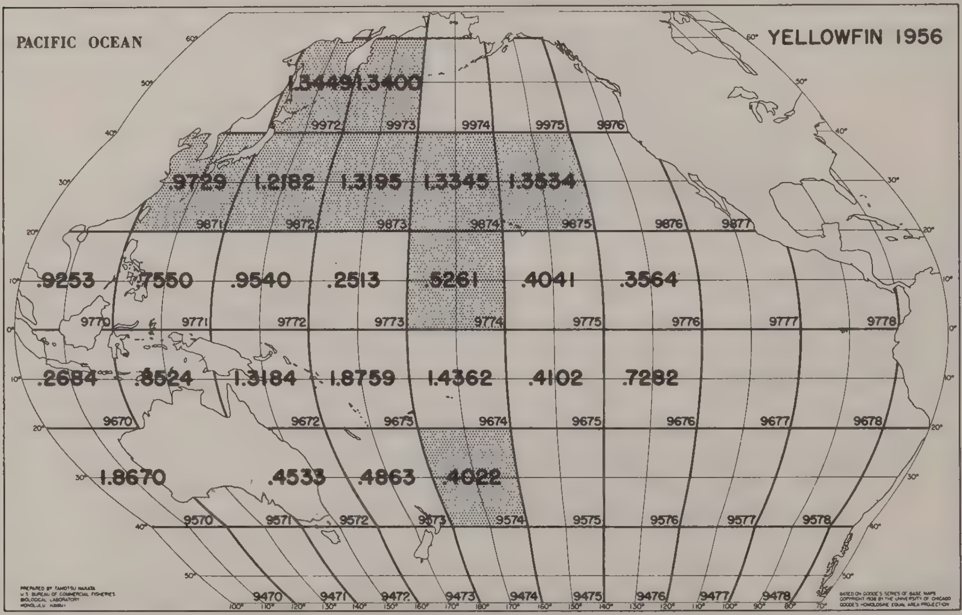
PACIFIC OCEAN
YELLOWFIN 1956
1.3449
1.3400
9972
9973
9974
9975
9976
.9729
1.2182
1.3195
1.3345
1.3534
9871
9872
9873
9874
9875
9876
9877
.9253
.7550
.9540
.2513
.5261
.4041
.3564
9770
9771
9772
9773
9774
9775
9776
9777
9778
.2684
.8524
1.3184
1.8759
1.4362
.4102
.7282
9670
9672
9673
9674
9675
9676
9677
9678
1.8670
.4533
.4863
.4022
9570
9571
9572
9573
9574
9575
9576
9577
9578
9470
9471
9472
9473
9474
9475
9476
9477
9478
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Figure 17d.--Yellowfin tuna, 1956: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

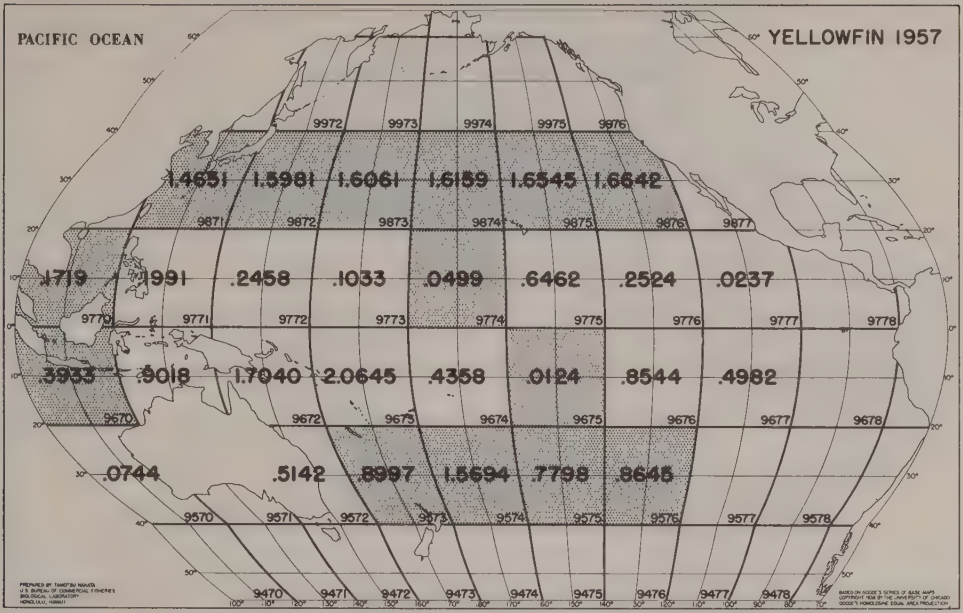
PACIFIC OCEAN
YELLOWFIN 1957
9972
9973
9974
9975
9976
1.4651
1.5981
1.6061
1.6159
1.6545
1.6642
9871
9872
9873
9874
9875
9876
9877
.1719
.1991
.2458
.1033
.0499
.6462
.2524
.0237
9770
9771
9772
9773
9774
9775
9776
9777
9778
.3933
.9018
1.7040
2.0645
.4358
.0124
.8544
.4982
9670
9672
9673
9674
9675
9676
9677
9678
.0744
.5142
.8997
1.5694
.7798
.8645
9570
9571
9572
9573
9574
9575
9576
9577
9578
9470
9471
9472
9473
9474
9475
9476
9477
9478
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Figure 17e.--Yellowfin tuna, 1957: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

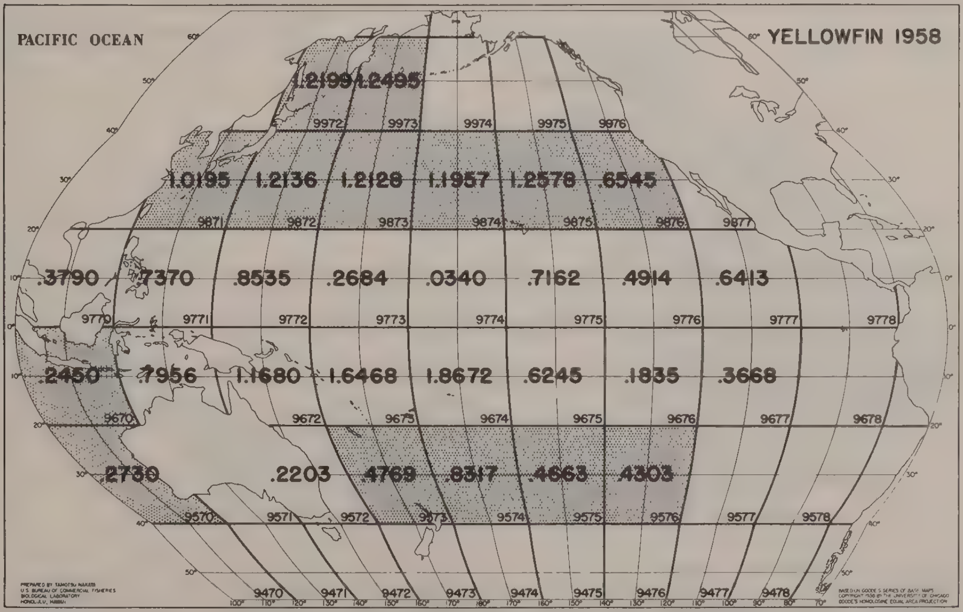
PACIFIC OCEAN
YELLOWFIN 1958
1.2199
1.2495
9972
9973
9974
9975
9976
1.0195
1.2136
1.2128
1.1957
1.2578
.6545
9871
9872
9873
9874
9875
9876
9877
.3790
.7370
.8535
.2684
.0340
.7162
.4914
.6413
9770
9771
9772
9773
9774
9775
9776
9777
9778
.2450
.7956
1.1680
1.6468
1.8672
.6245
.1835
.3668
9670
9672
9673
9674
9675
9676
9677
9678
.2730
.2203
.4769
.8317
.4663
.4303
9570
9571
9572
9573
9574
9575
9576
9577
9578
9470
9471
9472
9473
9474
9475
9476
9477
9478
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Figure 17f.--Yellowfin tuna, 1958: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

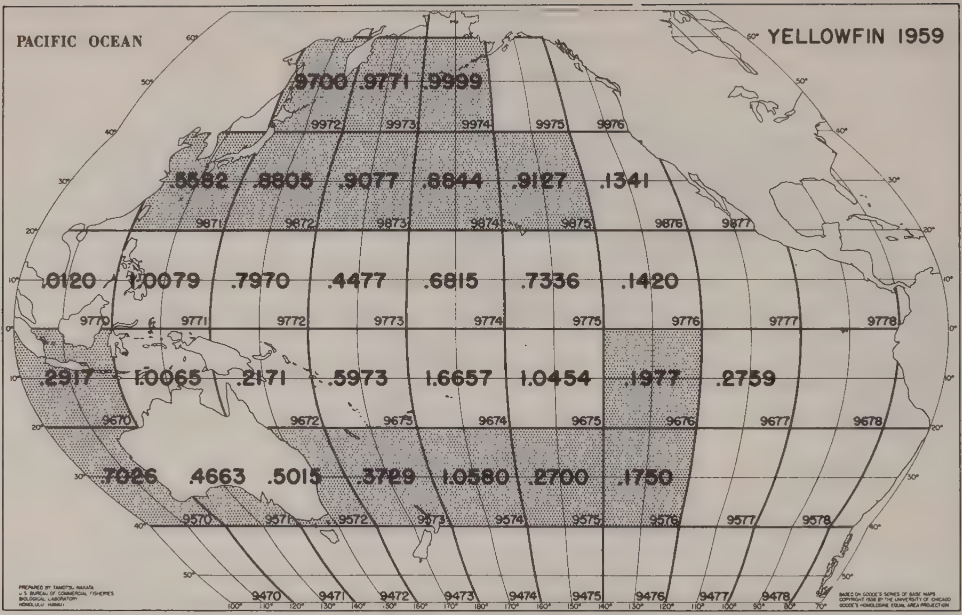
PACIFIC OCEAN
YELLOWFIN 1959
.9700
.9771
.9999
.5582
.8805
.9077
.8844
.9127
.1341
.0120
1.0079
.7970
.4477
.6815
.7336
.1420
.2917
1.0065
.2171
.5973
1.6657
1.0454
.1977
.2759
.7026
.4663
.5015
.3729
1.0580
.2700
.1750

Figure 17g.--Yellowfin tuna, 1959: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

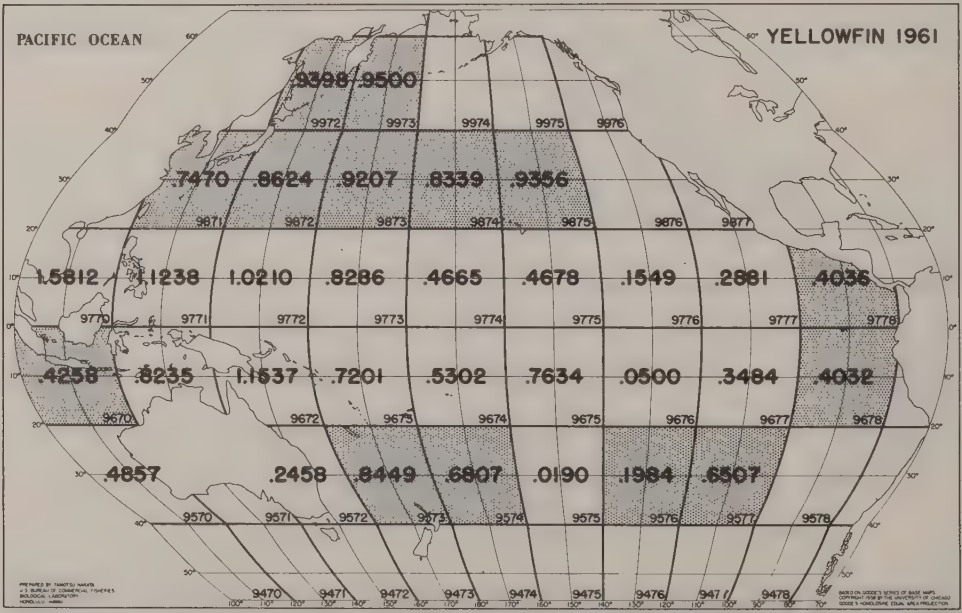
PACIFIC OCEAN
YELLOWFIN 1961
.9398
.9500
.7470
.8624
.9207
.8339
.9356
1.5812
1.1238
1.0210
.8286
.4665
.4678
.1549
.2881
.4036
.4258
.8235
1.1537
.7201
.5302
.7634
.0500
.3484
.4032
.4857
.2458
.8449
.6807
.0190
.1984
.6507

Figure 17h.--Yellowfin tuna, 1961: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

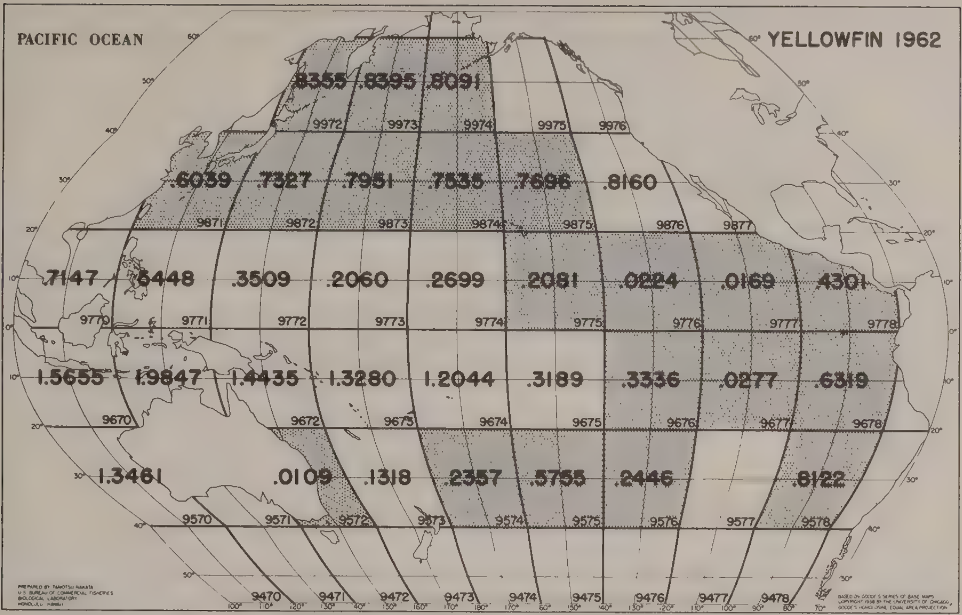
PACIFIC OCEAN
YELLOWFIN 1962
.8355
.8395
.8091
9972
9973
9974
9975
9976
.6039
.7327
.7951
.7535
.7696
.8160
9871
9872
9873
9874
9875
9876
9877
.7147
.6448
.3509
.2060
.2699
.2081
.0224
.0169
.4301
9770
9771
9772
9773
9774
9775
9776
9777
9778
1.5655
1.9847
1.4435
1.3280
1.2044
.3189
.3336
.0277
.6319
9670
9672
9673
9674
9675
9676
9677
9678
1.3461
.0109
.1318
.2357
.5755
.2446
.8122
9570
9571
9572
9573
9574
9575
9576
9577
9578
9470
9471
9472
9473
9474
9475
9476
9477
9478

Figure 17i.--Yellowfin tuna, 1962: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

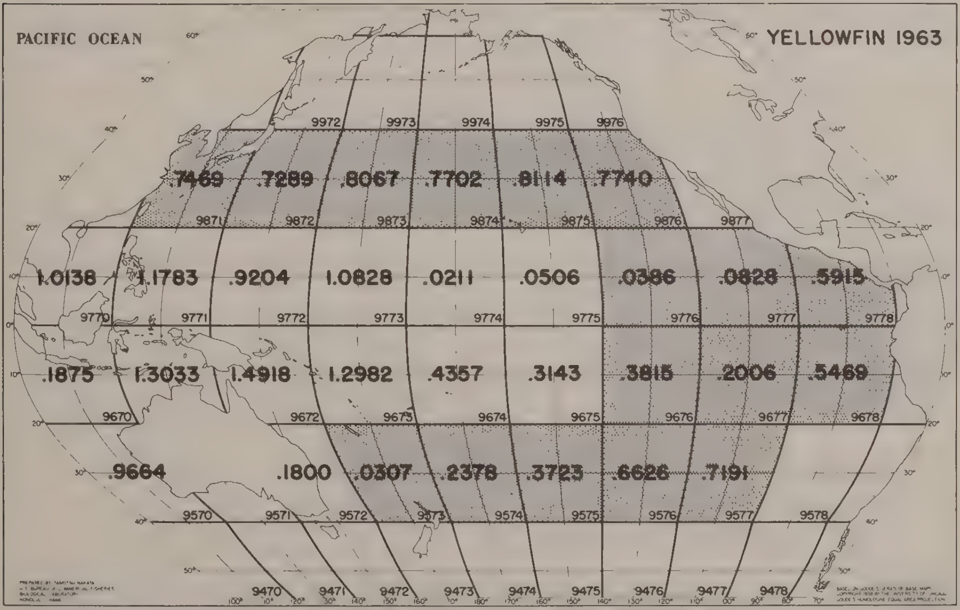
PACIFIC OCEAN
YELLOWFIN 1963
9972
9973
9974
9975
9976
.7469
.7289
.8067
.7702
.8114
.7740
9871
9872
9873
9874
9875
9876
9877
1.0138
1.1783
.9204
1.0828
.0211
.0506
.0386
.0828
.5915
9770
9771
9772
9773
9774
9775
9776
9777
9778
.1875
1.3033
1.4918
1.2982
.4357
.3143
.3815
.2006
.5469
9670
9672
9673
9674
9675
9676
9677
9678
.9664
.1800
.0307
.2378
.3723
.6626
.7191
9570
9571
9572
9573
9574
9575
9576
9577
9578
9470
9471
9472
9473
9474
9475
9476
9477
9478

Figure 17j.--Yellowfin tuna, 1963: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

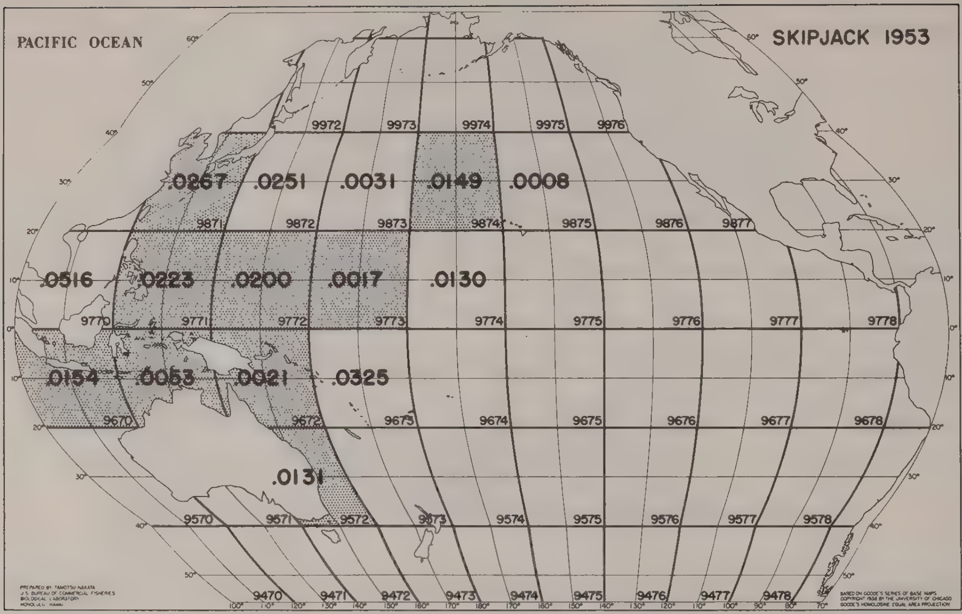
PACIFIC OCEAN
SKIPJACK 1953
9972
9973
9974
9975
9976
.0267
.0251
.0031
.0149
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Figure 18a.--Skipjack tuna, 1953: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

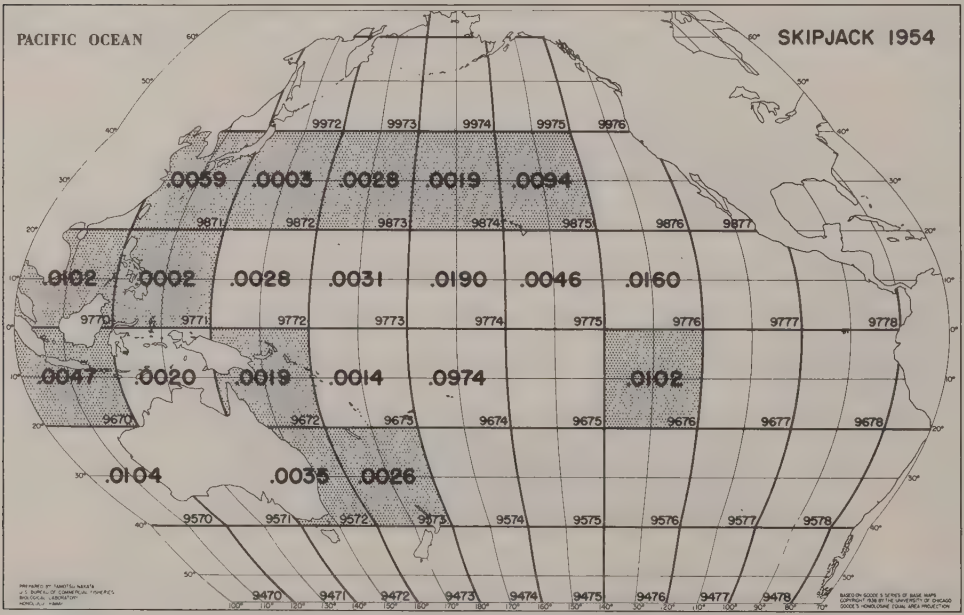
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Figure 18b.--Skipjack tuna, 1954: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

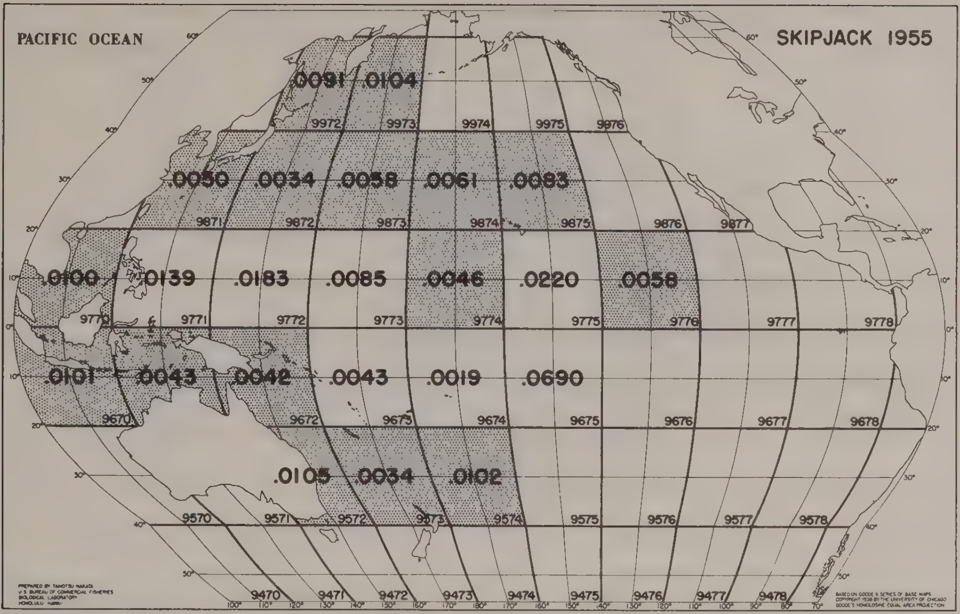
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Figure 18c.--Skipjack tuna, 1955: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

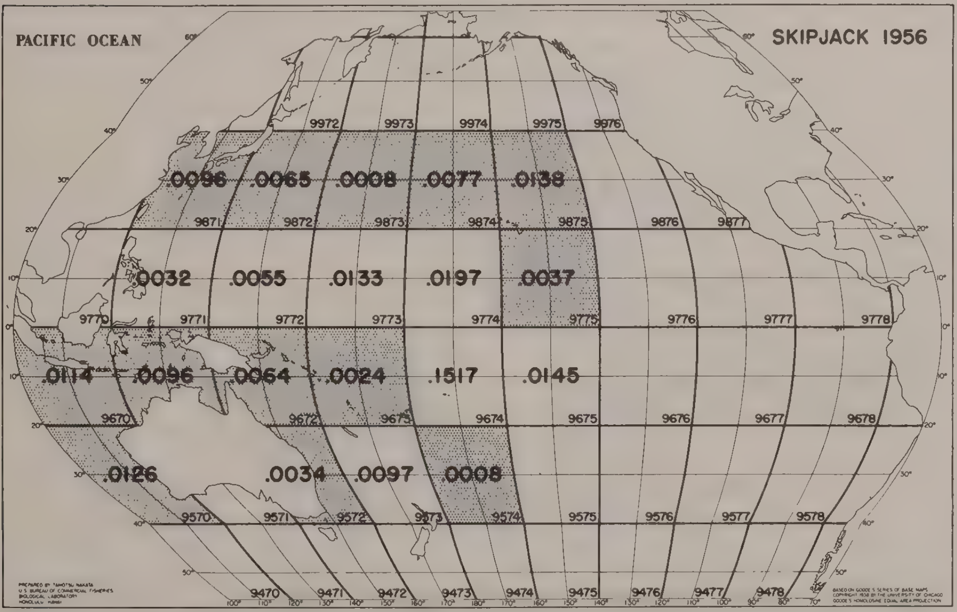
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Figure 18d.--Skipjack tuna, 1956: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

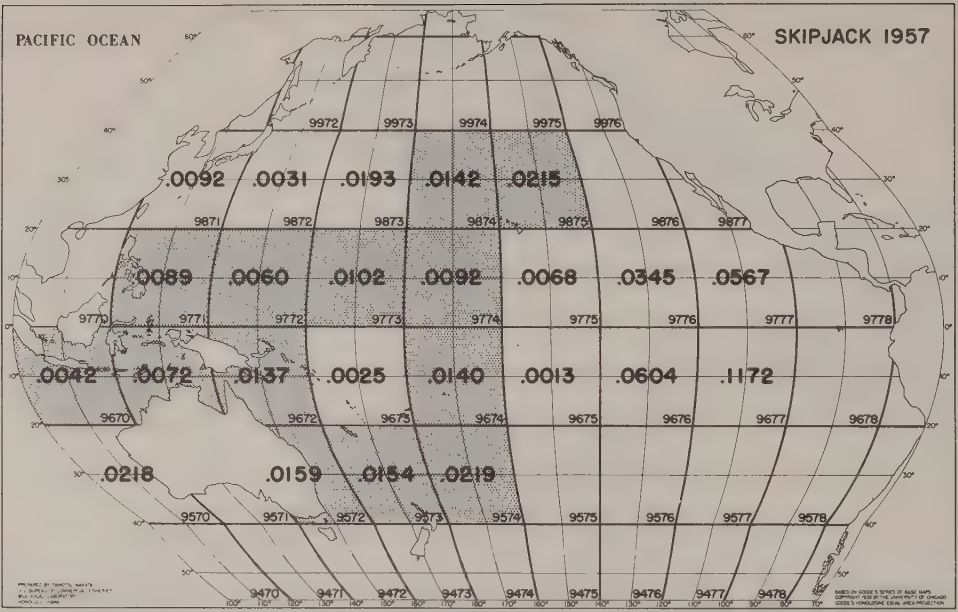
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Figure 18e.--Skipjack tuna, 1957: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

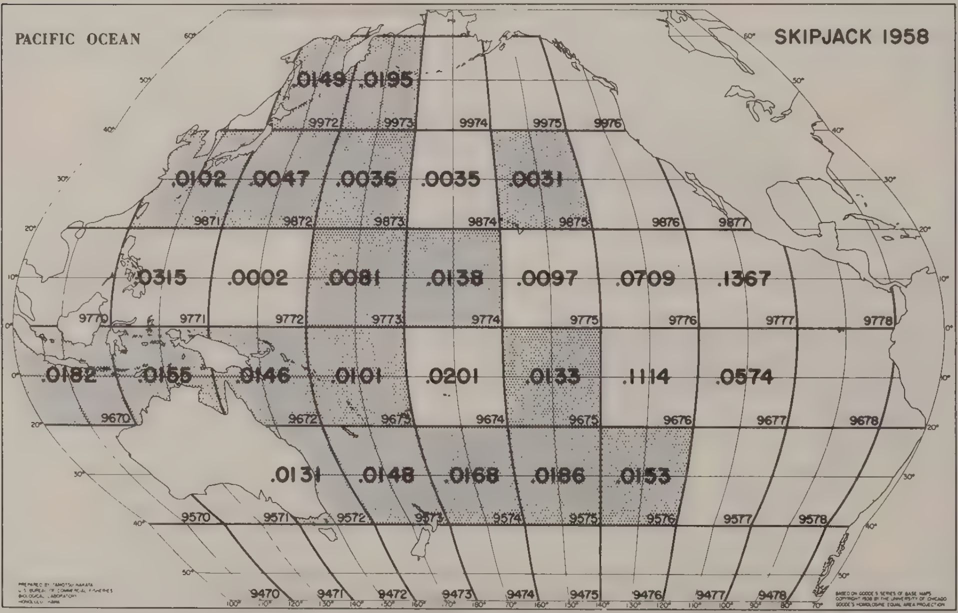
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Figure 18f.--Skipjack tuna, 1958: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

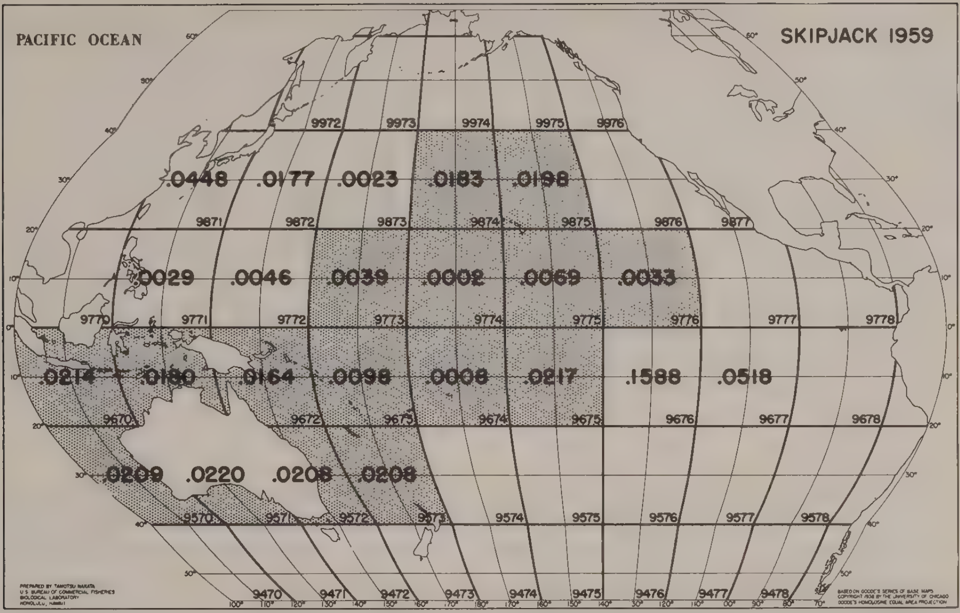
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Figure 18g.--Skipjack tuna, 1959: positive (unshaded) and negative (shaded) deviations of CPUE in different regions.

sect at the Hawaiian Islands. These data are given for 1953-64 in figure 19.

The monthly data show the same general temporal and spatial trends as the annual data. For example, in the two northern quadrangles the ratio of apparent abundance of bigeye tuna to apparent abundance of yellowfin tuna is much larger than in the two southern quadrangles, and the decline in apparent abundance of bigeye tuna in the post-1960 period is evident. In addition, the monthly data show that the degree of variability in CPUE tends to be proportionate to the CPUE.

The monthly data also demonstrate the effect of periodicities on annual averages (or for that matter, semiannual or quarterly averages). In a location where the season tends to be short the annual average CPUE, for example, will tend to be less than the annual average in a location where the season tends to be long; yet the apparent abundance for the short-season area might be much greater than the apparent abundance for any month in the long-season area. Although annual averages depict the general productivity of an area, shorter-term averages are needed to advise on fishing strategy. Estimation of the amplitude and frequency of the periodicities is clearly needed. The problems involved in this estimation are complex; no existing theory is entirely suitable for their solution.

PROBLEMS FOR FUTURE RESEARCH

We have seen that the contemporary center of apparent abundance is in the eastern Pacific for bigeye tuna and in the southwestern Pacific for yellowfin tuna. The apparent abundance of those sizes of skipjack tuna which are taken by

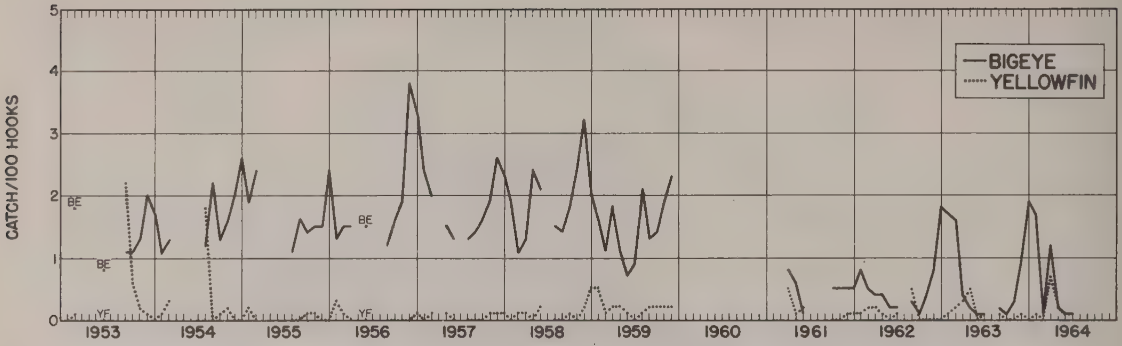

Figure 19a.--Catch of yellowfin and bigeye tunas per 100 hooks in quadrangle 9874, 1953-64.

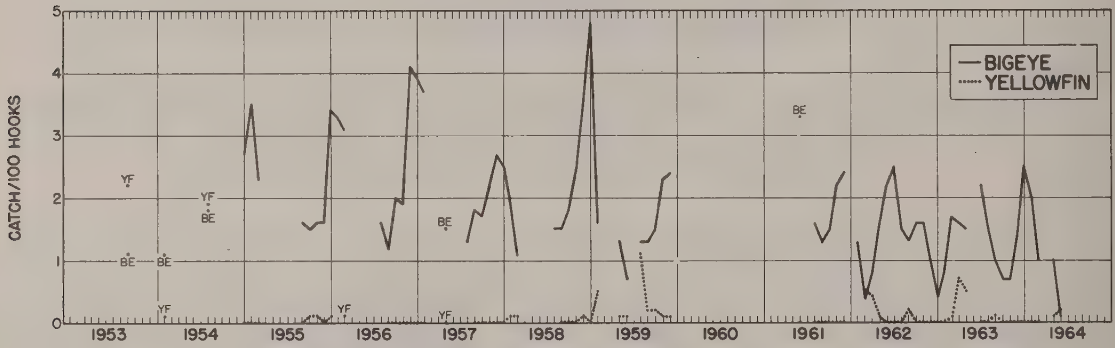

Figure 19b.--Catch of yellowfin and bigeye tunas per 100 hooks in quadrangle 9875, 1953-64.

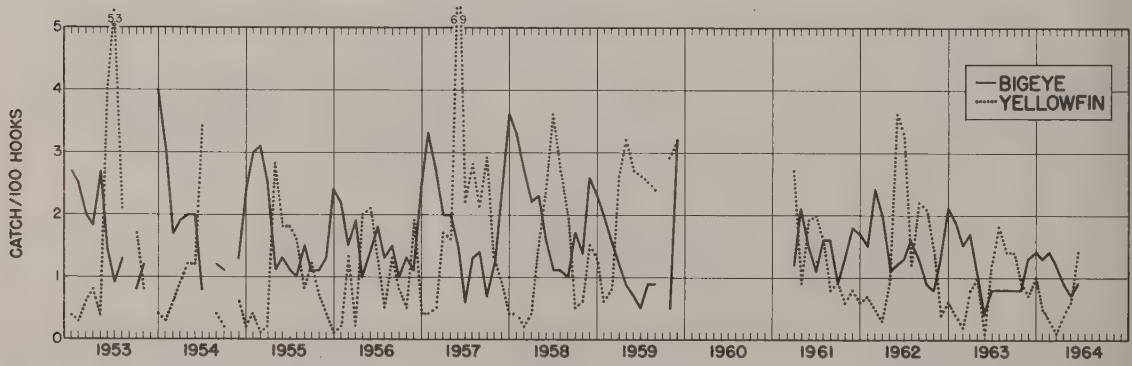

Figure 19c.--Catch of yellowfin and bigeye tunas per 100 hooks in quadrangle 9774, 1953-64.

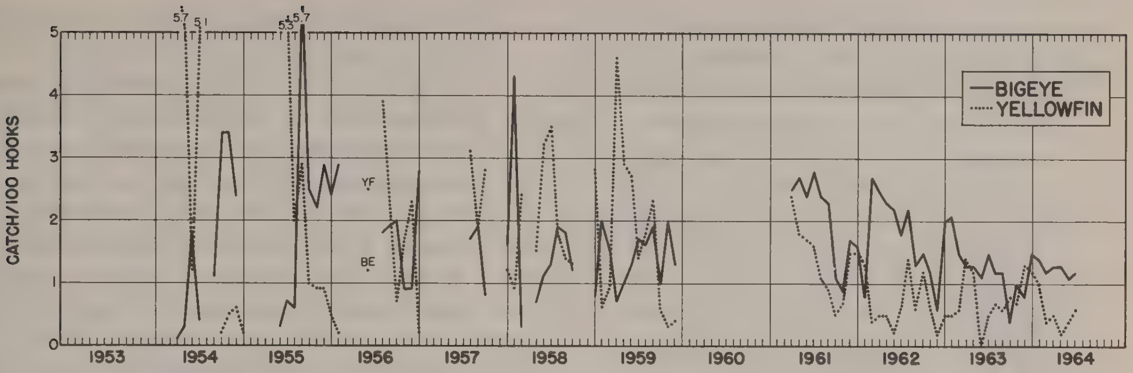

Figure 19d.--Catch of yellowfin and bigeye tunas per 100 hooks in quadrangle 9775, 1953-64.

longline gear is relatively high in the southeastern Pacific, a supposition which must be considered tentative. The apparent abundance of albacore is low in the equatorial region, but much higher to the north and south of the Equator.

It appears that the eastward expansion of fishing which is evident was encouraged by the high apparent abundance of bigeye tuna to the east. This shift is reflected in the distribution of the catch of bigeye tuna; the majority of the fish tended to be taken east of the location of major concentrations in effort. This point was discussed by Suda and Schaefer (1965a), who also pointed out that recent technological advances created increased demand for the bigeye tuna as a raw material for fish sausages. The apparent abundance of both bigeye and yellowfin tunas has tended to decline, particularly in the more recent years. It is necessary to relate these changes to the amount of effort expended. Although it is evident that the relative concentration of effort has been moving in an easterly direction it is necessary to place measures of effort in absolute terms so that we can examine, in some detail, the important relation between effort and CPUE. Despite the fact that this analysis has not yet been carried out for the entire Pacific, Suda and Schaefer (1965a) and Kume and Schaefer (1966) have demonstrated a negative relationship between CPUE and effort for the region east of long. 130° W. It is possible that a similar negative relationship will hold for the entire eastern Pacific.

For a fishing venture to be profitable the receipts accrued from a fishing trip must exceed the costs of the trip. The extent to which the cost of fishing in the eastern Pacific exceeds the cost of fishing in waters nearer to the Japanese archipelago is not certain, but the possibility is distinct that declining CPUE in the easterly extension of the fishery may result in declining receipts for vessel operations in this area. The result of such a situation, given that the fishery cannot compensate for declines in CPUE of one species by shifting to another, is likely to be a decrease and contraction of effort. If fishing has caused a decline in CPUE for bigeye tuna in the eastern Pacific, and if the areal extent of the fishery contracts in the same pattern in which it expanded, then it is evident that concentrations of effort would be drawn nearer to the Hawaiian Islands. Detailed studies of the Hawaiian longline fleet have been published for 1948-56 (Otsu, 1954; Shomura, 1959); it will be interesting to study the relation between the CPUE in the Hawaiian and Japanese longline fishery in the vicinity of the Hawaiian Islands subsequent to 1956, when relatively large increases in Japanese effort became evident in the quadrangles south of the Islands (9774 and 9775). (A more detailed study of the Japanese effort is needed to determine to what extent this increase was in the Hawaiian region rather than the equatorial region of these quadrangles.) Hida (1966) included measures of apparent abundance for the post-1956 period, but these are not comparable with the measures given by Otsu and Shomura.

Another problem is the measurement of the actual abundance of a species. The distributions implied in this paper are based only on measures of apparent abundance. Many of the problems involved in relating apparent abundance to actual abundance were discussed by Gulland (1964) and others in the symposium "On the measurement of fish stocks." In addition to relating apparent abundance to abundance, more detailed studies are needed of the CPUE statistic. Such questions arise as: To what are the statistical properties of the "ratio of averages" CPUE statistic? What is the relative efficiency of the various ratio estimators that can be used to estimate CPUE? What is the best method of estimating total catch and total effort? What is the amplitude and frequency of the oscillations in catch and effort? and What time and space stratification scheme will yield the best estimates of catch and effort for the more detailed analyses that these data require?

We have in our discussions tacitly assumed that the CPUE for each species is independent of the CPUE for any other species. Since several of the species harvested by longline are taken simultaneously in varying proportions on a gear with a well-defined and absolute maximum capacity, the postulate of independence is not likely. This problem may generate interpretive difficulties with regard to the effect of the albacore, for example, which has been treated in only a cursory fashion in this paper, on the distribution of catch and effort for the other species. For example, a gradual shift in emphasis of the fishery from one that attempts to catch only bigeye tuna to one that attempts to catch only albacore would produce, all other things being equal, a decline in apparent, but not actual, abundance of bigeye tuna. Fishes other than tunas, such as the billfishes, are not considered at all here. and data on sharks are not even a matter of published record. The problem of competition among several species for longline hooks has been considered by Rothschild (in press).

The density gradients implied by the increased apparent abundance of the bigeye tuna to the east and yellowfin tuna to the west also raise interesting questions with respect to the tendency for the size of both species to increase from west to east in the Pacific fisheries. (Recent discussions of these size gradients may be found in Suda and Schaefer, 1965b; Kume and Shiohama, 1965; and Kume and Joseph, 1966.) In the latest hypothesis on the subject, Suda and Schaefer (1965b) opined that this size gradient results from a vertical stratification in the size distribution of yellowfin tuna that is related to the depth of the mixed layer; the mixed layer becomes shallow to the east, but the longline gear fishes at a fixed depth, thus producing the east-west size gradient. By contrast with the yellowfin tuna the bigeye tuna occur in greatest apparent abundance in the region where the largest sizes of these fishes are taken, in the eastern Pacific (Kume and Shiohama, 1965). It should be noted, however, that this size gradient may not always obtain in the eastern portion of the eastern Pacific (Kume and Joseph, 1966). The question remains as to the location of the presumably large numbers of smaller bigeye tuna. Furthermore, since the average sizes of tunas can be reduced by fishing, the possibility that the east-west gradients are at least in part fishery-induced should be examined.

ACKNOWLEDGMENT

Thanks are due Gordon Broadhead for his critical reading of this paper.

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OBSERVATIONS ON THE ALEWIFE *(ALOSA PSEUDOHARENGUS)* IN CAYUGA LAKE[1]

Brian J. Rothschild
Research Assistant
Department of Conservation, Cornell University[2]

ABSTRACT

Observations on the seasonal movements, reproduction, phototaxis, and mass mortalities of the alewife were made at Cayuga Lake, New York, during 1960 and 1961. In Cayuga Lake the alewife winters in deep water and moves into the littoral area in the spring. This movement is accompanied by the onset of courtship behavior and then spawning. These reproductive activities are discussed. Fecundity estimates are given and hermaphroditism is mentioned. Positive phototactic responses of the alewife were noted except during the spawning period. The evidence on causes of mass mortalities in the alewife was reviewed, and it was concluded that variables other than temperature are involved.

The alewife (*Alosa pseudoharengus*) is one of the several species of anadromus fishes that have developed strictly fresh-water populations. One of these populations, in Cayuga Lake, New York, (Figure 1) was studied during 1960 and 1961. As a part of these studies the scale method was evaluated for determining the age of the alewife (Rothschild, 1963) and aspects of alewife population dynamics were considered (Rothschild, 1965). In addition observations were made on seasonal movements, reproduction, phototaxis and mass mortalities. These are reported here.

SEASONAL MOVEMENTS

The alewife winters in deep water (Breder and Nigrelli, 1936; Galligan, 1951; Gross, 1959). In the spring, when the water temperature approaches 50° F., alewives begin to move into the littoral area where courtship behavior becomes evident. Cessation of courtship in midsummer is accompanied by movements into deeper water. In Cayuga Lake the alewife moves into the littoral areas in late May and early June.

In 1960 alewives were first noticed on May 15 in the mouth of Interlaken Beach Stream. They may have been attracted by warm stream water (57° F.) flowing into the cooler lake (48° F.) (cf. Collins, 1952). Shore seining near the stream and at Taughannock Point yielded no alewives. By May 27 alewives were evident in nearly every stream mouth along the eastern shore of the lake. The lake temperature was 51° F. and stream temperatures ranged from 59° to 62° F. Seine hauls along beaches still did not yield alewives except in the immediate vicinity of stream mouths.

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[1] Derived from a Ph.D. thesis submitted to the Graduate School at Cornell University in 1962. The work was supported by National Science Foundation Grant 8909. The author is grateful to Dr. Edward C. Raney for criticism during the study and preparation of the manuscript. James Reckahn of Cornell University was most helpful with the field work.

[2] Present affiliation: U. S. Bureau of Commercial Fisheries, Biological Laboratory, Honolulu.

On the night of June 7, 1960, the Taughannock Point area was surveyed with a 10-ampere AC shocker from 9 p.m. to 1 a.m. The lake was 57° F. and Taughannock Creek was 62° F. Small alewife schools, about 10 to 15 feet in maximum dimension, were common in the lake. The main concentration was found in the warmer creek water from the stream mouth upstream to the first riffle area; the density of alewives in the stream was so great that distinct schools were not discerned. By June 11, the water had warmed to 64° F. and alewives were common nearly everywhere in shallow water.

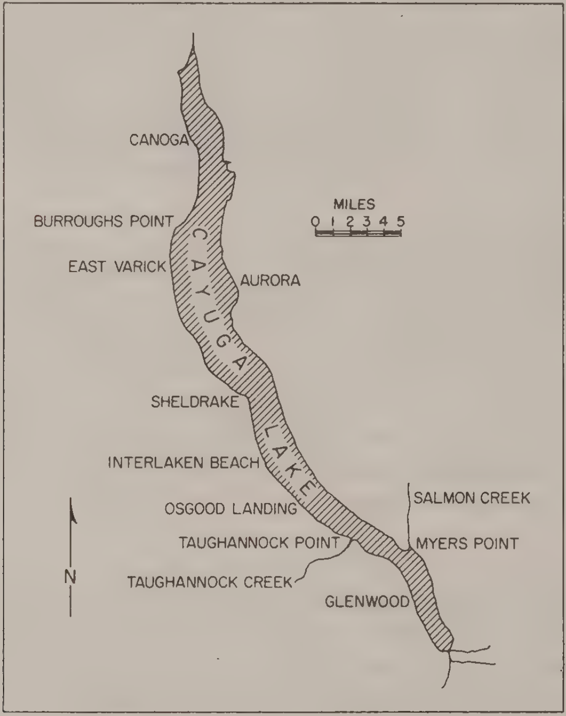
CANOGA
MILES
0 1 2 3 4 5
BURROUGHS POINT
EAST VARICK
AURORA
CAYUGA LAKE
SHELDRAKE
INTERLAKEN BEACH
SALMON CREEK
OSGOOD LANDING
TAUGHANNOCK POINT
MYERS POINT
N
TAUGHANNOCK CREEK
GLENWOOD

Figure 1. Map of Cayuga Lake.

At Canoga Island, which was not surveyed until midsummer in 1960, alewives were first evident in 1961 on May 12 when the water temperature was 52° F. and one specimen was taken. A few alewives were taken there on each of several subsequent nights (temperature 52°–56° F.) until the first week of June. Simultaneous seining at Taughannock Point yielded no alewives. By June 5 the water temperature had risen to 58° F. at Taughannock and several alewives were taken.

Alewives first appeared at Interlaken Beach Stream on June 3 in 1961 compared with May 15 in 1960. On June 3, 1961 the water temperatures of the stream and the lake were 59° F. and 50° F., respectively, and were approximately the same as the corresponding temperatures in 1960 when alewives first appeared in the stream. By June 12 the water temperature had risen to 69° F. at Canoga and 57° F. at Taughannock, and alewives were abundant at both locations. They became abundant on approximately the same date in both years.

Gross (1959) noted that alewives first appeared in the surface waters of Lake Hopatcong, New Jersey, in late April when the water temperature was 54° F. The first appearance of the alewife in Cayuga Lake was temporally later but at roughly the same temperature as Lake Hopatcong.

The increased apparent abundance of alewives in Cayuga Lake after the middle of June was accompanied by the onset of courtship and spawning activity. Alewives were generally abundant in the littoral areas until the first week in August. In early August they could only be taken in greatly diminished numbers in the littoral areas in the vicinity of Canoga and Taughannock Point. An offshore movement at this time may have been associated with completion of spawning or have been a reaction to warm surface water. Galligan (1951) presented data obtained through the operation of bottom-set gill nets which demonstrate that alewives in Cayuga Lake are found in deeper water as the seasons progress (Table 1).

TABLE 1. DEPTHS AT WHICH MAJOR CONCENTRATIONS OF ALEWIVES WERE ENCOUNTERED IN GILL-NETTING OPERATIONS FROM JUNE TO NOVEMBER IN CAYUGA LAKE*

Month	Depth in feet
June	20–70
July	20–60
August	40–200
September	40–180 and 40–120
October	50–260
November	160–230

* After Galligan (1951).

REPRODUCTION

Odell (1934b) reported spawning in the Finger Lakes from late May to mid-August. Spawning generally occurred in late May or early June (but, in one year, from July 9 to August 9) in Lake Ontario (Pritchard, 1929) and in late June in Lake Hopatcong, New Jersey (Gross, 1959). A marine population ascended a study stream in Maine from mid-May to mid-June (Havey, 1961). Gross indicated a water temperature of from 63° to 66° F. during initial spawning, and Havey's study showed that spawning runs occurred at from 50° to 60° F. Greeley (1938) observed alewives spawning at Lanoka Lake, New York, on July 15 when the water temperature was 73° F.

COURTSHIP BEHAVIOR

Entrance of alewives into the shallow water of Cayuga Lake was coupled with the onset of courtship behavior. Fish in the stream mouths were generally oriented in an upstream direction. A single fish would leave the oriented pattern and pursue another fish. Pursuits usually terminated without the pursuing fish approaching the pursued fish. Pursuits increased in frequency with time and warmer water. Several fish would appear to pursue a single individual. At times these fish would swim in a circular pattern, splash at the surface, and then disperse.

On occasion the pursued fish would not actively swim away, but would momentarily stop; at this time the pursuing fish would be side by side with or at a slight angle to the body of the pursued fish with its head at the level of the pursued fish's dorsal fin. All in the same instant the opercula of the pursued fish would appear to flare, and the pair would swim in a rapid helical or corkscrew pattern to the surface. At the surface the two fish would break the surface of the water with at least one on its side.

This so-called swirling behavior was infrequent when the fish first moved into shallow water but increased in frequency with time and warmer water. Early season "swirls" in water as shallow as 6 inches usually consisted of two fish, but as time progressed a swirl might consist of a group of several fish. When the surface temperature approached 70° F. alewives in Cayuga Lake moved out of the shallow water into deeper water. On the evening of July 5, 1961 the surface temperature was 68° F. at Taughannock Point. Alewives were at a depth where they could not be observed except when frequent "swirls" of large numbers of alewives would literally boil to the surface and immediately descend (perhaps a reaction to the warm surface water). There were perhaps a few hundred fish in each swirl. After August 3 in 1961 spawning behavior was no longer observed, but alewife eggs were collected in a plankton net set in 20 feet of water off Taughannock Point until August 7.

GONAD DEVELOPMENT

Pritchard (1929) and Graham (1956) observed that in Lake

Ontario male alewives matured at 3 years and females at 2 years of age. Gross (1959) suggested that alewives in Lake Hopatcong spawn only once.

Observations in Cayuga Lake indicated that males and females both matured at 2 years of age. There may be a difference in age at maturity, but this difference was not indicated in the samples. Since alewives of various ages were sexually mature in Cayuga Lake, it is presumed that they spawned more than once.

All male alewives of spawning age that entered the littoral area in the spring were in an advanced state of maturity. Testes were at a maximum size and milt was expressible from seminal tubules. Ovaries from 110 alewives were examined. Ovarian maturity increased with time. The first few females to enter the littoral area had cylindrical, elongate ovaries which contained many undeveloped ova.

The first large inshore movement of alewives consisted mostly of males. The few females contained ovaries which were nearly one-third as deep as they were long; the eggs were mostly immature. There were relatively few mature eggs in the posterior portion of the ovary. By late July and early August, females had increased in relative abundance and their ovaries were in an advanced state of maturity, being about one-third as deep as long and containing mature eggs which were mostly free of stroma. By the second week of August, the ovaries were spent and spawning was complete.

In a quiescent state the ovaries represented less than 1 per cent of the body weight. At maximum maturity in late July, the ovaries comprised about 4 or 5 per cent of the total body weight. When spawning was complete the whole visceral mass in both sexes became embedded in fatty tissue which presumably remained until gonadal activity the following spring.

Fecundity was measured by direct enumeration of mature eggs for six fish. The total length of each in millimeters together with its fecundity (in parentheses) were: 116 (8,180), 124 (7,771), 118 (9,040), 130 (5,796), 129 (7,581) and 124 10,011). Odell (1934b) gave the fecundity of 145-millimeter females (standard length) as 10,000 to 12,000 eggs.

Some male gonads were abnormal with one testis either atrophied, undeveloped or missing. There were four hermaphroditic examples in the 444 gonads examined. One hermaphroditic fish had ovarian material anteriorly and testicular material posteriorly. Fowler (1912) described a similar hermaphroditic American shad *(Alosa sapidissima)* from the Delaware River. Other hermaphrodites contained what appeared as male gonads on the right or left side and female gonads on the opposite side. Histologic examination of testicular material indicated the presence of sperm cells.

REACTION TO LIGHT

While in shallow water (during June and July), alewives exhibited no observable tactic response to light. Positive phototactic responses were evident as soon as movement to deeper water began. Kasahara (1961:122) reported that many fishes have a reduced phototactic response during spawning.

When the water surface was illuminated, alewives would aggregate immediately or in 1, 2, or sometimes even 3 hours. On some nights, particularly when the water surface was rough, aggregation would not take place. At first fish would splash, at the surface, on the periphery of the illuminated water. After a short time alewives would move in and out of the illuminated water, and concentration would begin at a depth of 10 to 15 feet under the light. Schools would frequently come to the surface and immediately descend to the original depth. It is not known whether the movement of alewives into the illuminated area was an actual tactic response or involved feeding. At times adults were clearly feeding on young-of-the-year alewives. The young of the year were close to the surface, and the adults would ascend for brief intervals to feed. Predation may have been great, but it was inefficient since many "strikes" by adults at young resulted in the young escaping. Small numbers of large common shiners (*Notropis cornutus*) and young American smelt (*Osmerus mordax*) were frequently taken with the alewives Smelt are usually considered as negatively phototactic.

MASS MORTALITIES

Entrance of alewives into littoral areas may be coupled with mass mortalities. Graham (1956) described the annual mass mortalities of the alewife in Lake Ontario, reviewed literature pertinent to the phenomenon, and suggested lethal temperatures as a causal factor.

Odell (1934a) noted that mass mortality of the alewife occurred only occasionally in Seneca Lake, New York, and suggested that it results from a population imbalance due to large year classes. Gross (1953) reported early summer mass mortalities to be nonexistent in Lake Hopatcong, New Jersey. Residents along Cayuga Lake have reported only occasional mass mortalities, and many have the impression that the frequency of mortalities decreased after intensive stocking of lake trout (*Salvelinus namaycush*) which are extensive predators of alewives. Alewives in the Finger Lakes pass through essentially the same time-space-temperature gradient as those in Lake Ontario.

It seems odd that fish which are capable of discriminating fine differences in temperature should enter and remain in a lethal-level gradient. Brett (1959) pointed out that fish in nature are usually found well within their zone of thermal tolerance. But Ferguson (1958) showed in laboratory experiments that yellow perch (*Perca flavescens*) entered and remained in lethal temperature gradients; the perch, however, may have been crowded. In another experiment Collins (1952) demonstrated a preference of the alewife for the warmer of two temperature alternatives.

Graham (1956) performed laboratory experiments which indicated that the alewife had an upper lethal tolerance of approximately 23° C. (about 73° F.), but Trembley (1960) reported field observations where alewives were found in a lagoon of the Delaware River which had a temperature gradient from 80° to 90° F. When these alewives were frightened into the warmer water of the lagoon, some died of "heat shock". On July 1, 1961, alewives were observed in daylight in Interlaken Beach Stream which had a surface temperature of 79° F. Discrepancies in lethal temperature reports are probably associated with acclimation phenomena.

Both Graham (1956) and Odell (1934a) noted that some moribund alewives had infestations of *Saprolegnia*. Observations in 1960 were made on the first day alewives entered into shallow water at Interlaken Beach when temperatures of the lake and stream were 48° F. and 57° F., respectively. Schools contained individuals that were moribund and heavily infested with fungus (presumably *Saprolegnia*). Unless the onset of fungus infestation and moribund condition had been instantaneous, mortality-inducing variables must have been operative before the alewives entered the shallow, relatively warm water. The lethal level of temperature at this time, if temperature was the cause of death, could have been no higher than 57° F. Many dead alewives were observed in Cayuga Lake until the middle of July.

In 1961 no dead or dying alewives were observed in Cayuga Lake. The spring warming pattern in 1961 was essentially the same as that in 1960, but it took place about 2 weeks later. Temperature may be a factor in mass mortality of alewives, but other factors are certainly involved.

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PRELIMINARY ASSESSMENT OF THE YIELD POTENTIAL OF THE SKIPJACK TUNA IN THE CENTRAL PACIFIC OCEAN[1]

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ABSTRACT

At the present state of our knowledge, any estimates of the yield of skipjack tuna (Katsuwonus pelamis) from the central Pacific must be speculative. It is desirable, nevertheless, to select a reasonable range within which the yield potential is likely to fall. It appears that if the skipjack tuna that migrate from the eastern Pacific fishery area to the central Pacific could be harvested, the annual catch of 68,000 metric tons could be increased 2 to 17 times. The total potential of the central Pacific may be still greater since this area is almost certainly inhabited by skipjack tuna that do not circulate through the eastern Pacific fishery.

INTRODUCTION

One of the goals of the Governor's Conference on Central Pacific Fishery Resources was to estimate the magnitude of the skipjack tuna resources of the central Pacific. The present paper is a formulation of some of these estimates. It is based on the hypothesis that the skipjack tuna (Katsuwonus pelamis) taken in the coastal fisheries of the eastern Pacific are spawned in the equatorial central Pacific, migrate to the eastern Pacific fishery areas, remain there a relatively short time, and then return to the central Pacific to spawn (see Kawasaki, 1964, and Rothschild, 1965). This hypothesis implies that the skipjack tuna that enter the eastern Pacific are subject to fishing mortality only when they are actually in the eastern Pacific fishery areas, since we assume that the numbers taken in the high-seas areas of the central Pacific are negligible. Therefore, the skipjack tuna that leave the eastern Pacific fishery area can be considered as an escapement stock that inhabits the central Pacific. In the central Pacific, the escapement stock almost certainly mixes with skipjack tuna that never circulate through the eastern Pacific fishery area, and therefore estimates of yield based on escapement stock must be underestimates. The primary objective of the present paper is to consider the yield potential of the escapement stock, should the fishery be modified so that it would continue to harvest these fish during their movement to, and in, the central Pacific. Since there is not yet sufficient information to provide a point estimate of the yield potential of the escapement stock, let alone for the entire Pacific, the approach taken here will be to attempt to select a reasonable range within which the yield potential of the escapement stock is likely to fall and then to comment briefly on the possible relation between the yield potential of the eastern Pacific escapement stock and the skipjack tuna stocks for the entire Pacific Ocean.

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[1] This paper is based on exercises that were prepared for oral presentation at the Governor's Conference. It was written at the request of the conferees, who felt that a document describing the presentation might be useful. In the present state of our knowledge, any estimates of skipjack tuna yield in the central Pacific is acknowledgedly speculative.

YIELD POTENTIAL OF THE ESCAPEMENT STOCKS

For this preliminary assessment, conjectured but reasonable coefficients of growth and mortality are employed to estimate yield by means of the equation developed by Beverton and Holt (1957). The yield function for various combinations of the coefficients is conveniently tabulated in Beverton and Holt (1964). The notation which follows is standard or defined in the text. We need initially:

M = instantaneous coefficient of natural mortality;

F = instantaneous coefficient of fishing mortality;

Z = instantaneous coefficient of total mortality;

E = rate of exploitation;

t_o, K, L_∞ = constants of the von Bertalanffy growth equation;

A_0 = set of population parameters $\left\{M_0, E_0, L_\infty, K_0\right\}$;

Y'_0 = a dimensionless index of yield per recruit, under assumption A_0 and given exploitation sizes as defined and tabulated by Beverton and Holt (1964).

In order to assess the yield potential of the escapement stock Y'_0 is computed under two conditions:

1) Under the first condition Y'_0 is computed over the interval between age (length) at recruitment and age (length) at escapement. Under this condition Y'_0 is denoted by Y'_{01}.

2) Under the second condition Y'_0 is computed over the interval between age (length) at recruitment and maximum age (length). Under this condition Y'_0 is denoted Y'_{02}.

Clearly, the ratio $R_0 = Y'_{02}/Y'_{01}$ gives a measure of the relative change in yield that can be expected should a fishery continue to harvest--under a fixed A_0--the escapement stock. Note that since Y'_{01} is dimensionless, so is R_0. We assume that, as in many fisheries, stock sizes remain within a range where their effect on recruitment is, on the average, undetectable. Application of R_0 to the yield of an existent steady-rate fishery that operates under A_0 and condition 1 would provide an absolute measure of potential yield, should the fishery continue to operate under A_0 but extend its fishing, under condition 2, to the larger and older members of the escapement stocks.

Parameters for the Yield Equation

To obtain values of R_0 we need to obtain reasonable A_0 and the size ranges over which the fish are exposed to fishing. It must be emphasized that at this stage of our understanding of the biology of skipjack tuna, the choice of A_0, recruitment size, and escapement size is largely conjectural. A discussion of the choice of growth coefficients, size at recruitment and escapement, and mortality coefficients follows.

GROWTH COEFFICIENTS

The von Bertalanffy growth coefficients of $K = 0.7$, $L_\infty = 85$ cm., and $t_0 = 0$ will be used throughout this paper. These are similar to those given by Rothschild (as reported by Shomura, 1966). Although Rothschild's estimates were based on incremental growth from a relatively few tag returns and must be considered tentative since the growth estimation study is not yet complete, it appears that the growth curve with these coefficients as parameters is in good agreement with other estimates of growth from tag returns (Schaefer, Chatwin, and Broadhead, 1961) and modal progressions (Kawasaki, 1963). The growth curve given by Brock (1954), however, implies a faster rate of growth than that tentatively proposed by Rothschild; therefore if Brock's curve is the more accurate estimate of growth, use of Rothschild's curve for yield calculations would tend to produce conservative estimates.

RECRUITMENT AND ESCAPEMENT SIZES

The sizes at recruitment and escapement are critical parameters in making the yield estimates, since the amount of time a fish spends in the fishery area, susceptible to fishing mortality, is a function of recruitment and escapement sizes. A notion of these sizes for the northern fishery area of the eastern Pacific can be obtained from graphs presented by Broadhead and Barrett (1964). Length distributions of the catch in the southern fishery area (south of the Gulf of Tehuantepec) are not available in the literature and therefore we must assume that the length distribution of the catch in the southern area is approximated by the length distribution of the northern area. The Broadhead and Barrett graphs show that the fork length of skipjack tuna in the Baja California region, for example, ranges from about 41 to 65 cm. and averages about 53 cm. (Since an important proportion of the eastern Pacific catch in the northern area is taken from the Baja California region, it appears that the length frequencies for the entire northern region of the fishery would be weighted toward the Baja California frequencies.) A striking feature of these lengths is that they appear to vary little among the quarter-years for which the length frequencies are presented. One of several possible interpretations of this phenomenon (Rothschild, 1965) is that it reflects size- (or age-) specific movements through the fishery. The difference between the maximum and minimum lengths provides an estimate of the amount of time a skipjack tuna spends in the eastern Pacific (i.e., the time required for a 41-cm. fish to attain a length of 65 cm.). According to our assumed von Bertalanffy growth curve, this time would be slightly more than 1 year. If we interpret the apparent stability in size distribution to be a result of size- (or age-) specific movement, then an estimate of slightly more than 1 year must be an upper bound on the eastern Pacific sojourn time (sojourn time is defined as the amount of time a fish spends in the fishery area, whether it leaves as a result of mortality or emigration). On the other hand, a more accurate estimate of sojourn time might be obtained from the mortality coefficients of skipjack tuna. (Only Z will be considered in this paper since it is the only parameter that we will use, explicitly, to obtain yield from R_0 and estimation of Z alone requires fewer restrictions than an estimate of both F and M.) Estimates of survival rates of skipjack tuna from tagging experiments were provided by Schaefer, Chatwin, and Broadhead (1961). Fink (1965) modified their procedure of estimation to account for variations in fishing intensity upon the tagged fish. He used their data and additional data to provide two estimates of Z (corrected for tag shedding by assuming that the coefficient of tag shedding in skipjack tuna is the same as that estimated for yellowfin tuna, Thunnus albacares). He obtained a Z value of 5.92 for taggings in the Baja California area in 1957 and 3.96 for taggings off northern Peru in 1955-60. The latter estimate was annotated as "unreliable." As Fink notes, these rather high values of Z are probably the result of emigrations from the fishery as well as deaths. We will therefore denote a Z that represents both emigration losses and mortality decrements as $\tilde{Z}$. If we take Fink's estimate at face value to represent the loss of tagged fish from all causes other than tag shedding, and assume that the behavior of the tagged fish is not different from that of the untagged fish, then we can use $\tilde{Z}$ to estimate the average sojourn time in the eastern Pacific. This estimate can be made if we assume that the waiting time until a tagged fish leaves the fishery, either as the result of death or emigration, follows the exponential probability law (this is analogous to the usual deterministic assumption that the rate of loss is proportional to the number present) with parameter $\tilde{Z}$. The mean of this distribution is $\tilde{Z}^{-1}$ and therefore with $\tilde{Z} = 5.92$, the average sojourn time in the fishery is about 2 months. Correspondingly, the average sojourn time off northern Peru (based on the data for 1955-60) is about 3 months. To translate the average sojourn time into a recruitment and escapement size we use the expression $t' = \bar{t} - Z^{-1}$ (Beverton and Holt, 1956), where t' is the average size at recruitment, and $\bar{t}$ is the average length of the fish in the fishery. If we use Fink's not-unreliable $\tilde{Z}$ and take $\bar{t}$ to correspond to a length of 53 cm. (17 months) we derive a t' of 15 months, which corresponds to a length of 50 cm. A 50-cm. skipjack tuna grows, according to our growth assumption, about 3 cm. in 2 months and therefore we take the average size at entrance and exit, to the nearest values tabulated in Beverton and Holt (1964), as 0.58 L_∞ (49.3 cm.) and 0.62 L_∞ (52.7 cm.), respectively.

Since an average eastern Pacific sojourn time of 2 months seems rather short and is based on only 1 year's tag returns, we will also make yield computations, for comparative purposes, with a perhaps more conservative, but arbitrarily selected, sojourn interval of about 6 months, which would correspond to an average entrance size of 0.54 L_∞ (45.9 cm.) and an exit size of 0.68 L_∞ (57.8 cm.).

TOTAL MORTALITY RATES

Two approaches can be considered for the estimation of total mortality rate Z. In the first we can attempt to determine the amount by which $\tilde{Z}$ overestimates Z. For example, owing to a lack of data, it was necessary for Fink to apply to skipjack tuna the instantaneous tag shedding coefficient ($Q = 1.06$) determined for yellowfin tuna. Clearly, if Q is larger than 1.06 for skipjack tuna, a positive bias in the estimate of Z will result. Unfortunately no data are available to determine if $\widetilde{Z}$ is positively or, for that matter, negatively biased as the result of using the coefficient obtained for yellowfin tuna. Another clue to a component of $\widetilde{Z}$ which might cause overestimation may be obtained from the assertion, which needs to be studied critically, that the length distribution of skipjack tuna in the eastern Pacific is relatively stable. Stability in length could be utilized to provide a lower bound estimate of an average instantaneous rate of emigration. To make this estimate simply, we assume that the stable length distribution has an approximately normal distribution with a mean length corresponding to the mean length of the catch (53 cm.) and a standard deviation (6 cm.) which is approximately one-fourth of the range of fish lengths. According to the growth curve which we have adopted in this paper a 53-cm. skipjack would grow about 2 cm. in 1 month. From tables of the normal probability distribution we can ascertain that a normal distribution ($\mu = 55$, $\sigma = 6$) would extend about 13 percent of its area to the right of a normal distribution with $\mu = 53$, $\sigma = 6$. The 13-percent extension implies that 13 percent of the fish present in month X reach lengths in month X + 1 that would not be included in a normal distribution with $\mu = 53$, $\sigma = 6$. This would correspond to a loss by emigration associated with the increase in size of 13 percent per month or an instantaneous loss-rate coefficient of 1.7 per year.

In the second approach we can attempt to obtain a direct estimate of Z. We again use the relationship that $Z = (\bar{t} - t')^{-1}$. Clearly we have, at present, no way of estimating the average age or age at recruitment for the entire population, but from our knowledge of the structure of the population we could surmise what might be a likely range. For example, the average length of the population is probably in the 60- to 65-cm. range and the average length at recruitment is probably in the 45- to 50-cm. range. Using the assumed growth curve and $Z = (\bar{t} - t')^{-1}$ we find that these ranges correspond to $1 \leq Z \leq 2$. The formula for Z is, of course, sensitive to slight changes in recruitment and average age and further requires the assumption that Z is constant throughout the life of the steady-state population.

Yield Estimates

Values of the R_0 were computed as a function of Z for sojourn times of 2 months (estimated from the mortality coefficient in Fink's tagging study) and 6 months (arbitrarily chosen). These values are plotted in figure 1. For the shorter time, $1 \leq Z \leq 2$ generates a seventeenfold to fivefold increase in steady-state yield; for the 6-month interval, $1 \leq Z \leq 2$ generates a sixfold to twofold increase in yield. Thus, if the fishery could harvest--under a fixed A_0--the escapement stock, then we would expect anywhere from a twofold to seventeenfold increase in yield of skipjack tuna. This would correspond to increased annual catches of 140,000 to 1,190,000 tons (using 70,000 tons as an average steady-state yield).

We can conclude that, if all of our assumptions are reasonable, there is a potential for an increased yield; it is, in fact, possible that this potential could be large. The results emphasize the importance of the sojourn time and show that, at least theoretically, knowledge of the sojourn time is at least as important as knowledge of mortality rates. If the

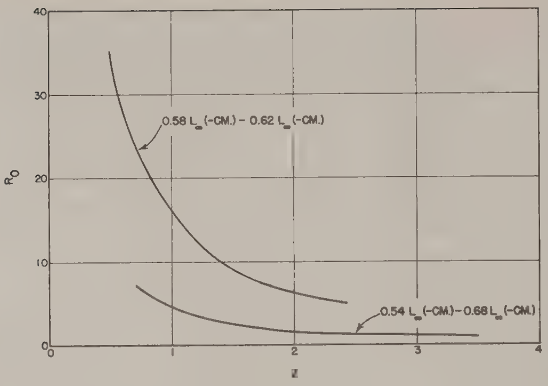

Figure 1.--Values of R_0 (ratio of yields under whole-life exploitation to yield under limited-life exploitation) as a function of Z under two recruitment-escapement size assumptions. Upper curve is for assumed sojourn time of 2 months, lower curve for 6 months.

actual sojourn time in the eastern Pacific is about 2 months, we could conservatively expect to triple or quadruple the present yield by extending exploitation to the west.

DISCUSSION

It is obvious that at present we lack the right kinds of data to provide firm estimates of the magnitude of the escapement stock. We have relied on a tentative estimate of growth, a single "mortality" coefficient to estimate immigration-emigration sizes, and surmised estimates of total mortality. In addition it was necessary to apply length-frequency distributions from the Baja California region to both the southern and northern fishery areas of the eastern Pacific. For this preliminary assessment, we have not considered the effects of varying A_0 as the fish move from the eastern to the central Pacific, the effect that fishing in the central Pacific might have on recruitment to the eastern Pacific, or the problem of optimum yields.

It is emphasized that these estimates of yield potential are strictly of the escapement stock and therefore must be underestimates of the yield potential for the central Pacific, since this area is almost certainly inhabited by skipjack tuna that do not circulate through the eastern Pacific fishery areas. In this connection Rothschild (1965) has hypothesized that the skipjack tuna of the Marquesas-Tuamotu region do not enter the eastern Pacific fisheries. If this hypothesis is correct, the skipjack tuna that inhabit this vast area of the South Pacific must comprise an as yet unexploited population.

The harvesting of the escapement skipjack tuna raises certain practical problems connected with the logistics of the fisheries. One of these problems involves the density of the escapement fish in the central Pacific. At least two factors may tend to reduce density in the central Pacific relative to density in the eastern Pacific: (1) since the escapement fish are older than the sizes fished, their numbers are certainly less; and (2) since the area of the central Pacific is larger than the eastern Pacific fishery area, it is conceivable that the escapement skipjack tuna are spread over a much larger area than the one now fished. On the other hand, the biomass of the older escapement population might be larger than that of the younger fished population; congregating mechanisms which would tend to increase density almost certainly operate in the central Pacific (see, for example, Sette, 1955); and escapement fish might be mixed with nonescapement skipjack tuna to provide densities which would enable profitable fishing.

The dynamics of the skipjack tuna, when interpreted on a recruitment-escapement basis, generate a set of problems similar to those that occur in the interpretation of salmon dynamics (see Hirschhorn, 1966). The emigration of skipjack tuna from the fishery area appears to be correlated with the onset of sexual maturity (Rothschild, 1965)--a phenomenon which is the reverse of that described by Beverton (1963) for clupeids, where the entrance of certain clupeids into the fishery is correlated with the onset of sexual maturity.

In conclusion, we can note that information available to estimate the yield potential of the escapement stock is limited, but it can be seen that the escapement fish could contribute to a possibly substantial increase in the present catch of skipjack tuna. The largest unknown remains, however; the proportion of the biomass of marketable-size skipjack tuna of the central Pacific that are escapement fish. A perhaps more direct approach to the problem would be to devise a method for directly estimating the biomass of skipjack tuna in the central Pacific and its size composition.

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CORRELATION BETWEEN OCEANOGRAPHIC FACTORS AND ABUNDANCE OF THE FLORIDA RED-TIDE (*GYMNODINIUM BREVE* DAVIS), 1954–61

GEORGE A. ROUNSEFELL and ALEXANDER DRAGOVICH

CORRELATION BETWEEN OCEANOGRAPHIC FACTORS AND ABUNDANCE OF THE FLORIDA RED-TIDE (*GYMNODINIUM BREVE* DAVIS), 1954–61[1]

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Abstract

Data on the Florida red-tide organism, *Gymnodinium breve* Davis, and concomitant oceanographic measurements from February 1954 through July 1961 were analyzed to determine effects of certain environmental factors on abundance. A multiple curvilinear correlation showed that 61 per cent of the monthly variability in abundance of *G. breve* was associated with variations in salinity, temperature, onshore winds of over 7 kts, and abundance the previous month. Correlation was attempted between the residuals of this multiple correlation and nine chemical variables: PO_4-P, total PO_4-P, NO_3-NO_2-N, copper, alkalinity, silicon, calcium, total organic nitrogen, and ammonia NH_3-N. No correlations were significant.

Introduction

Blooms of the red-tide organism, *Gymnodinium breve* Davis, have caused mass mortalities of fish on the west coast of Florida from Florida Bay and Key West north almost to Cedar Key—also along the coast of Texas from Freeport south to Mexico, extending down the coast of Tamaulipas. Heavy fish kills in Florida have occurred chiefly between Anclote Key and Cape Romano.

This paper estimates the degree of association between the abundance of the causative organisms, *G. breve,* in the Anclote Key-Cape Romano area, and certain environmental factors on which data were collected concomitantly over the period February 1954 through July 1961, by biologists of the Bureau of Commercial Fisheries. The analysis was prepared under Contract 14-17-0002-97 between the Bureau of Commercial Fisheries, U. S. Fish and Wildlife Service, and the University of Alabama.

Dr. Charles L. Seebeck, Professor of Mathematics and Director of the University of Alabama Computer Center, and Dr. Paul M. Hummel, Professor of Business Statistics, advised on statistical procedures. Dr.

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Hummel and Mr. William J. Gray wrote the computer programs. Mr. Hugh A. McClellan, Mr. Walter R. Nelson, and the staff of the computer center assisted in computer operations. Mr. James E. Sykes, Chief of the Bureau of Commercial Fisheries Biological Station at St. Petersburg Beach, gave advice in conduct of the project. Dr. Joseph H. Kutkuhn reviewed the manuscript. Mr. Robert D. Kelly and Mr. Walter R. Nelson prepared the illustrations. The types of observations available and the periods covered (except for a few months in which certain observations were not made) are as follows:

SAMPLING DATA AVAILABLE FOR THIS REPORT

Item	Period covered	
	From	To
Counts of *G. breve*	February 1954	July 1961
Salinity	do.	do.
Water temperature	do.	do.
Wind	do.	do.
Inorganic PO_4-P	September 1955	March 1960
Total PO_4-P	do.	July 1961
Nitrate-nitrite nitrogen	do.	do.
Total dissolved copper	July 1957	December 1959
Alkalinity	April 1960	July 1961
Silicon	do.	do.
Calcium	do.	do.
Ammonia, NH_3-N	do.	do.
Total organic nitrogen	January 1961	do.

TREATMENT OF DATA

The naked dinoflagellate, *G. breve,* is so fragile that counts must be made of living cells. At very low concentrations of organisms, cells are often found in one or more of the six to ten, 1-ml aliquots pipetted from the surface of a sample (usually 2 liters of water in an Erlenmeyer flask, placed under lights for several hours prior to examination to concentrate the organisms at the surface), but no cells are found in aliquots taken from the sample after it has been mixed. In the published sources of data listed such samples are designated as P to indicate the presence of *G. breve,* but the count is given as O. In our analysis those samples were given a minimum value of 0.1 per ml.

The frequency distributions of counts of *G. breve* are extremely skewed; counts ranged from 0 to 16,000 per ml, with the mode close to 0. To use such distributions in correlation analyses a transformation is required. In a preliminary analysis (Rounsefell & Nelson, 1964) a logarithmic transformation was used in which 1.0 was added to each sample to give a value to all samples, and thus eliminate multiplication by zero. Although this

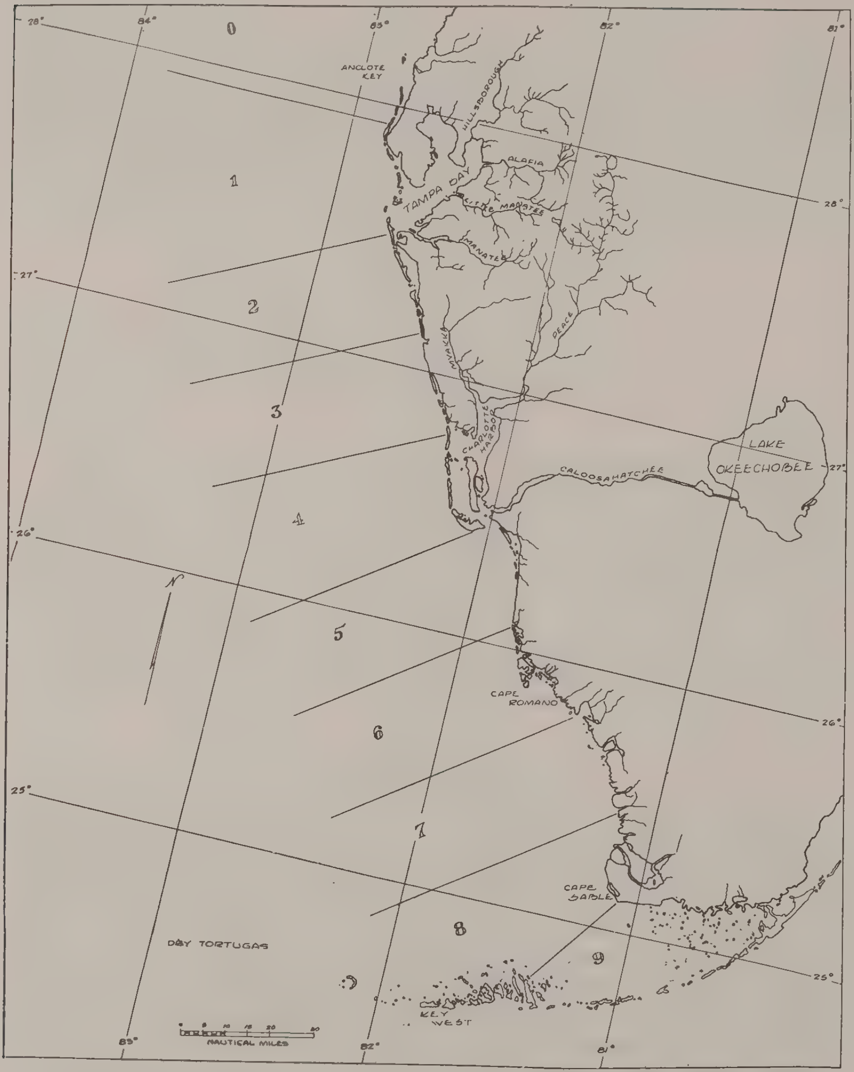
28°
84°
0
83°
ANCLOTE KEY
82°
81°
HILLSBOROUGH
ALAFIA
TAMPA BAY
LITTLE MANATEE
MANATEE
1
28°
27°
2
MYAKKA
PEACE
3
CHARLOTTE HARBOR
LAKE
OKEECHOBEE
27°
CALOOSAHATCHEE
4
26°
N
5
CAPE ROMANO
6
26°
25°
7
CAPE SABLE
8
DRY TORTUGAS
9
25°
KEY WEST
NAUTICAL MILES
83°
82°
81°

FIGURE 1. North-south areas used in coding of Florida red-tide data.

procedure worked reasonably well, it gave too high a value to the low counts. In this report we have minimized this error by using the count per centiliter, rather than per milliliter. The addition of 1.0 to all sample counts per centiliter has no practical effect on the statistical analysis.

TABLE 1

DISTRIBUTION OF MONTHLY MEANS OF *G. breve* SAMPLES
(Log of geometric mean of X + 1 per centiliter)

Logarithm of geometric mean	Seasons					Relative abundance used in analyses
	March-May	June-August	September-November	December-February	Total	
0.000-0.000	2	5	2	3	12	1
.001- .025	3	4	1	2	10	2
.026- .050	1	3	3	4	11	3
.051- .080	4	5	1	1	11	4
.081- .125	5	1		1	7	5
.126- .200	4	2		1	7	6
.201- .300	1	1	3	2	7	7
.301- .450			2	3	5	8
.451- .675		1	3	1	5	9
.676-1.050					0	10
1.051-1.800	1	1	2	1	5	11
1.801-3.000	1		3	3	7	12
Total	22	23	20	22	87	

Almost all samples were taken in daylight; consequently any bias that might be introduced through the probability of vertical diurnal movement, or scattering in the dark hours, was greatly reduced.

In the earlier years of the present study, most stations were sampled only at the surface; later, samples were usually taken at both surface and bottom; and in more recent years, intermediate depths were also usually sampled. Even during the period when surface and bottom samples were taken, however, the bottom sample was often omitted. Only surface samples were used in the statistical treatment of *G. breve* data, however, because they were available at all stations throughout the period, and were more consistent than subsurface samples.

A preliminary computer analysis by Rounsefell & Nelson (1964) showed that the heavy concentrations of *G. breve* tended to closely parallel the shoreline. The density of organisms was never great outside the coastal band extending from 4 miles inside of the passes to 15 miles offshore. Nor did heavy concentrations occur north of area 0 or south of area 6 (Fig. 1).

The monthly mean log (log of the geometric mean) of the individual samples, plus 1.0, was computed for both the northern areas (0 to 2) and the southern areas (3 to 6), omitting means based on less than ten samples. The means are given in Figure 2, in which the cross-hatched areas are for months associated with fish kills. This figure emphasizes the extreme positive skew of the data far too extreme to transform into a curve approaching the normal through a logarithmic transformation.

TABLE 2
DENSITY OF *G. breve* IN RELATION TO OBSERVED SALINITY AND TEMPERATURE IN INDIVIDUAL SURFACE SAMPLES

Salinity ‰ or Temperature °C.	Salinity				Temperature			
	September-February		March-August		September-February		March-August	
	N	Log (X + 1) / N	N	Log (X + 1) / N	N	Log (X + 1) / N	N	Log (X + 1) / N
<11	8	0	4	0	26	0.305		
11	6	0	7	0	22	.212		
12	11	0	9	0	59	.500		
13	8	0	4	0	108	.304		
14	9	0	10	0	98	.460	1	0
15	11	0	11	0	135	.568	9	1.517
16	5	0	16	0	140	.829	23	.441
17	6	0	11	0	162	.958	54	.114
18	11	0	10	0	195	.548	87	.185
19	12	0	9	0	276	.330	103	.167
20	17	0	9	0	253	.464	111	.083
21	15	0.257	24	0.013	324	.385	97	.111
22	22	0	19	.032	395	.518	130	.114
23	19	0	26	.067	356	.444	175	.062
24	35	.221	34	.102	329	.524	185	.086
25	41	.218	36	.017	216	.590	224	.053
26	48	.072	48	.034	88	.389	220	.031
27	58	.257	62	.034	158	.381	290	.039
28	67	.389	80	.061	272	.336	341	.072
29	79	.593	91	.113	339	.205	670	.061
30	147	.451	117	.148	187	.216	785	.039
31	250	.500	187	.146	53	.034	416	.052
32	414	.788	280	.126	4	0	100	.009
33	512	.938	381	.149	5	0	38	.003
34	682	.801	522	.121			5	0
35	819	.215	548	.064				
36	615	.048	741	.008				
37	118	.014	413	.021				
38	27	0	151	0				
39	18	0	50	0				
40	4	0	18	0				
41	5	0	13	0				
42	12	0	6	0				
43	3	0	6	0				
44	2	0	1	0				
45	1	0	3	0				
46	1	0						
47			5	0				
48			4	0				
49	1	0	2	0				
50			1	0				

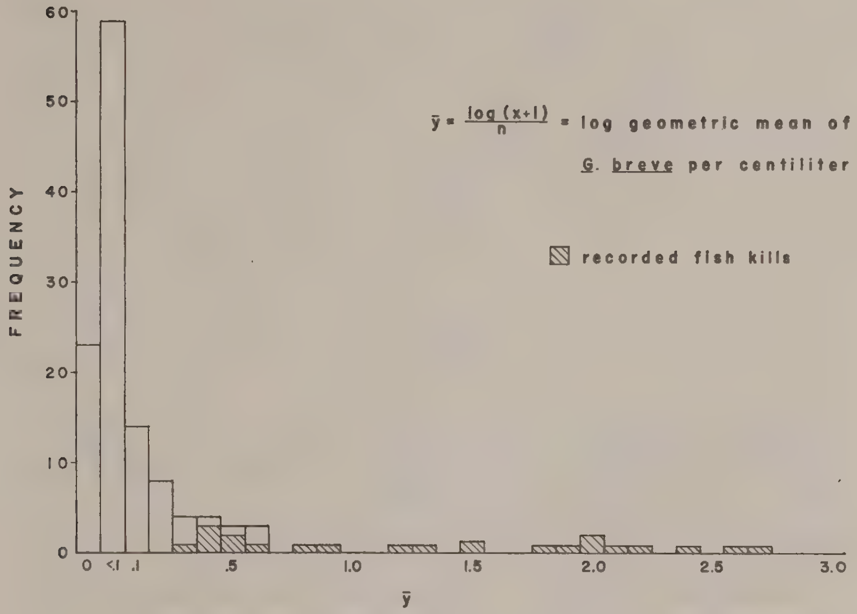

FIGURE 2. Frequency distribution of monthly means of *G. breve* per centiliter for grouped north-south areas 0 to 2 and 3 to 6, restricted to a coastwise band from 4 miles inside of the passes to 15 miles offshore.

Sampling during the earlier years of the study was somewhat heavier in areas 3 to 6, and after 1958 almost all sampling was in areas 0 to 2. To obtain a sufficiently long time series it was necessary to combine the data for areas 0 through 6. The frequency distributions by seasons of these combined (weighted) means are shown in Table 1.

The logarithmic scale in Table 1 (column 1) was divided into increasingly larger intervals to overcome the extreme positive skew illustrated by Figure 2. Each of the 12 empirical divisions was then assigned a rank (column 7) which was used as the abundance rating for *G. breve* throughout the correlation analyses.

It will be noted in Table 1 that the 6-month period from September through February contained 9 of the 12 monthly means with very high *G. breve* densities (ranks 11 and 12); and only 8 of the 22 months with very low densities (ranks 1 and 2). This suggests that environmental conditions were more favorable to *G. breve* during the period September through February.

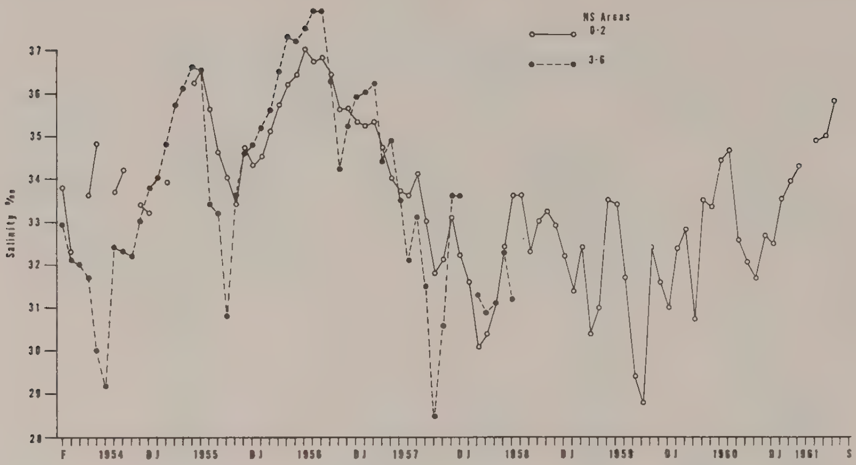

FIGURE 3. Mean monthly salinity for grouped north-south areas 0 to 2 and 3 to 6.

EFFECTS OF SALINITY AND TEMPERATURE

It was apparent from the preliminary analysis that both salinity and temperature play important roles in determining the abundance of *G. breve*. Since it was important to be able to combine the 0-2 and 3-6 areas to obtain a long-term series, we compared the mean monthly salinities in the two areas (Fig. 3). During the period when both areas were sampled the salinities corresponded rather well. Long-term trends in salinity are apparent; high values in late 1955 and 1956 are followed by a long steady decline.

The range of salinity tolerated by *G. breve* is shown in Table 2. The total range in which live organisms were found extended from 21‰ to 37‰. The upper limit of salinity at which appreciable numbers of organisms occurred was 35‰. The lower limit of salinity was not as well defined (Fig. 4); although densities decreased at salinities below 27‰, the occurrence of organisms at low densities at salinity as low at 21‰ suggests that these lower ranges may inhibit multiplication but permit survival.

The range of temperature tolerated by *G. breve* (Table 2 and Fig. 5) is rather wide. Organisms were found at 10° to 33°C. The upper favorable limit appears to lie between 29° and 30°C. The lower temperature limit for growth, as for salinity, is not clearly defined. Although organisms were found at temperatures as low as 10°C, the steep slope of the density curve (Fig. 5) suggests that temperature becomes successively more inhibiting below 15°C.

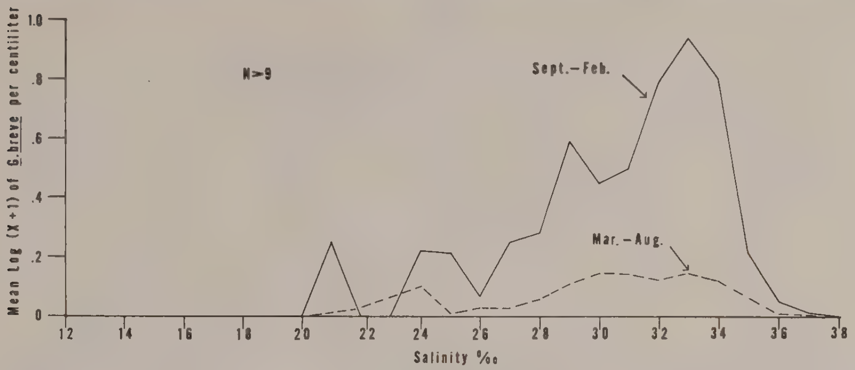

FIGURE 4. Means of *G. breve* per centiliter in individual surface samples by parts per thousand salinity.

Some interaction appears to exist between salinity and temperature. Figure 6 shows the monthly density ranking of *G. breve* (see Table 1) plotted against mean monthly salinity and temperature for the months with heavy, medium, and light blooms that occurred during the 87 months covered by the data. Blooms at low salinities appear to be favored by higher temperatures and vice versa.

SELECTION OF VARIABLES

The preliminary analysis made it clear that the density of *G. breve* is dependent upon several factors. Furthermore, the relations with environ-

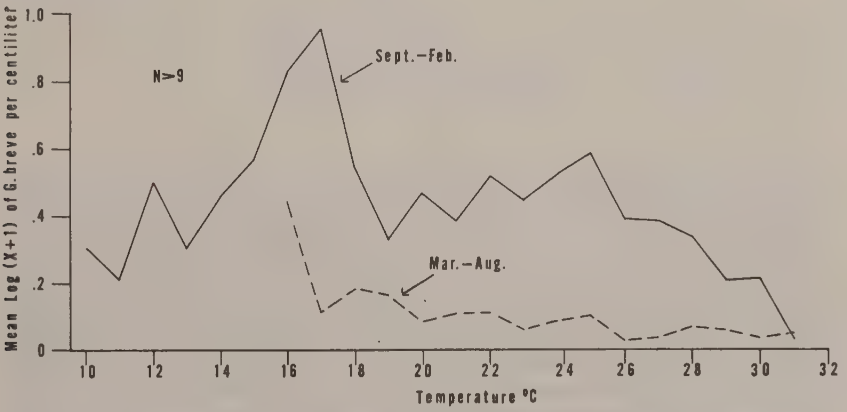

FIGURE 5. Means of *G. breve* per centiliter in individual surface samples by degrees of temperature.

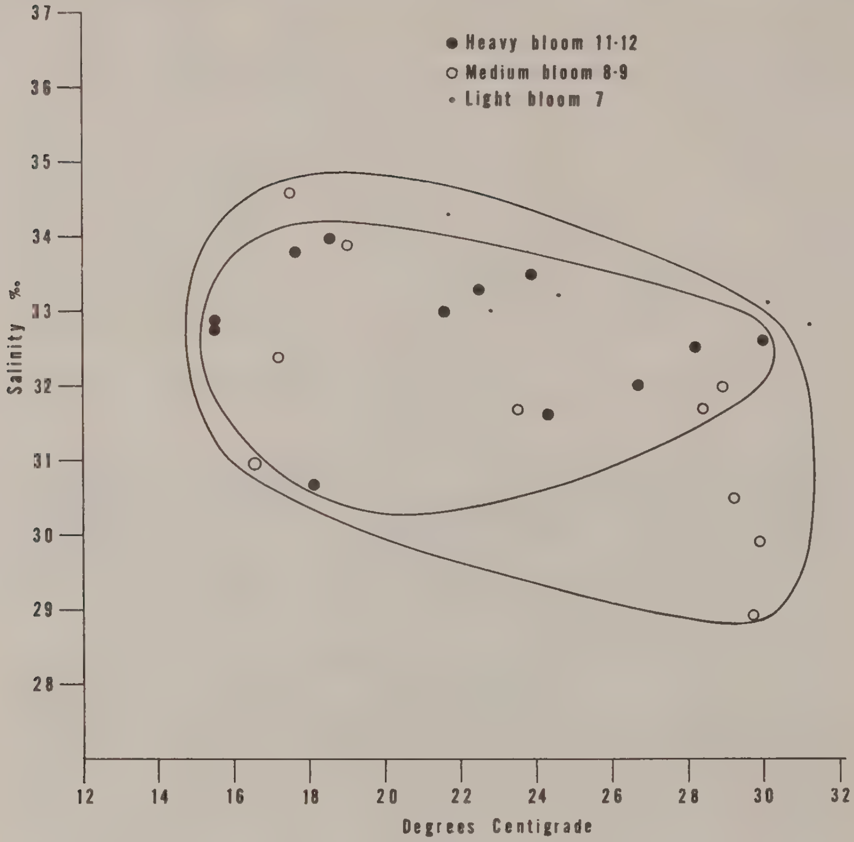

FIGURE 6. Mean monthly abundance rankings of *G. breve* for bloom stages versus temperature and salinity.

mental factors are not only nonlinear, but they appear to react with one another, thus obscuring their effects. For these reasons a multiple curvilinear correlation analysis was made of the chief factors measured. The importance of salinity and temperature has already been shown.

The importance of wind in encouraging or dispersing blooms has been suggested by several authors. Many have mentioned the role of winds in creating convergences. Pomeroy, Haskin, & Ragotzkie (1956) suggested that winds act as a concentrating agent for the organism. Since the effect of wind deserved consideration, records of wind direction, velocity, and duration at the Tampa International Airport were obtained from the U. S. Weather Bureau.

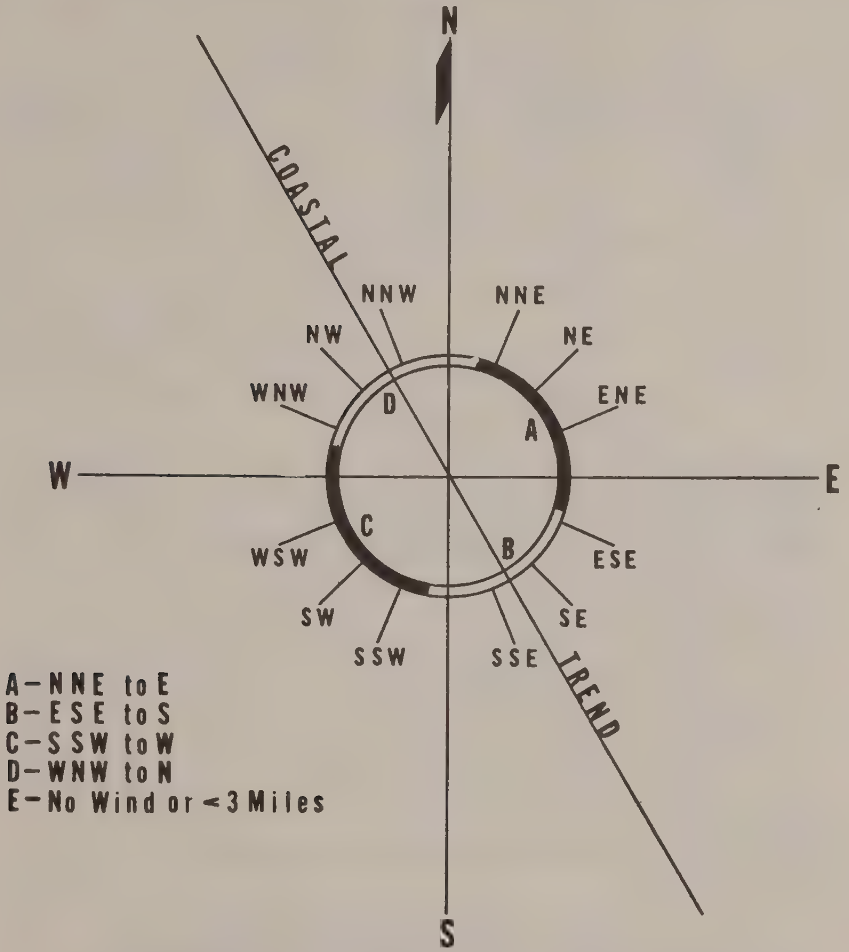
N
COASTAL
NNW
NNE
NW
NE
WNW
ENE
D
A
W
E
C
WSW
B
ESE
SW
SE
SSW
SSE
TREND
A—NNE to E
B—ESE to S
C—SSW to W
D—WNW to N
E—No Wind or <3 Miles
S

FIGURE 7. Relation of coastal trend to wind direction sectors.

The effect of winds on density of *G. breve* was difficult to determine accurately because each oceanographic station usually was sampled only once each month. Since short-term effects could not be considered, all analyses dealt with monthly averages. The relation of the trend of the coastline to wind direction is shown in Figure 7, which also shows the sectors by which the data were analyzed. The data were tabulated by hours per month (adjusted to 744 hours, or 31 days), sector, and velocities in knots of 0-3, 4-7, 8-12, 13-18, and 19 plus. Because of the bulk, the original data are not presented here.

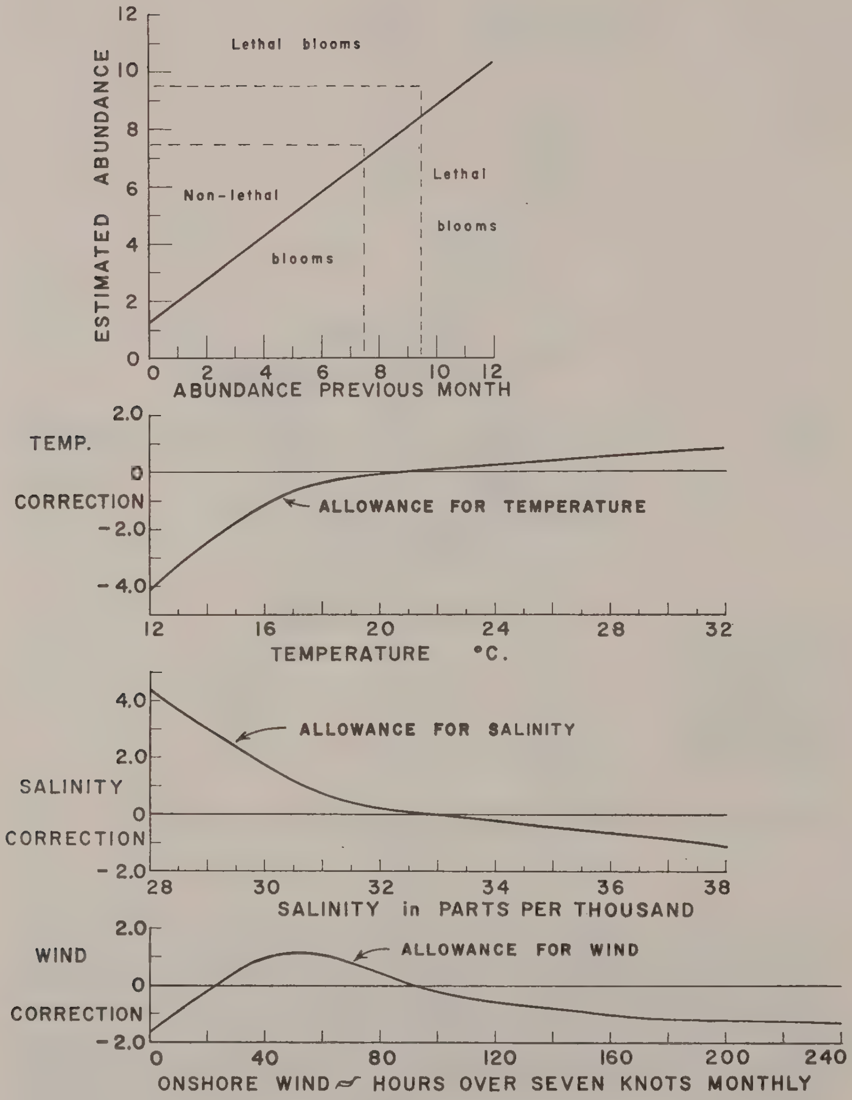

FIGURE 8. Nomograph for estimating abundance ranking of *G. breve* from results of a multiple curvilinear correlation analysis.

TABLE 3

CORRELATION OF MONTHLY ABUNDANCE RANKING OF *G. breve* WITH CERTAIN VARIABLES

Independent variables	Correlation	Degree of association	Standard error of estimate
Previous month's density of *G. breve*	[1]0.7542	0.569	2.275
Salinity, wind, and temperature	[2]0.6227	0.388	3.338
Salinity, wind, temperature, and density of *G. breve* for previous month	[2]0.7817	0.611	2.106

[1] Correlation coefficient, r.

[2] Index of multiple correlation (Ezekiel, 1941).

Several preliminary plots of hours of wind per month from different direction sectors were plotted against the mean monthly density rankings of *G. breve* from areas 0-6, including the coastal band from 4 miles inside of the passes to 15 miles offshore. These plots of grouped averages show that the density of *G. breve* appeared to be affected chiefly by onshore winds. Winds from sectors B, C, and D combined showed an effect, but the greatest effect came from the onshore winds of sector C alone. We therefore elected to include the hours of onshore wind from sector C as one of the independent variables in the multiple correlation analysis.

Still another variable considered was the density of *G. breve* during the previous month. In laboratory experiments by W. B. Wilson (Minutes of the Red Tide Symposium, at Galveston, Texas, 1958) the average rate of division of *G. breve* was 0.4 per day; therefore, it seemed logical to expect some correlation between the density of organisms from one month to the next.

MULTIPLE CURVILINEAR ANALYSIS

By the successive-approximation methods of Ezekiel (1941), the four above-mentioned independent variables—salinity, temperature, wind, and the previous month's abundance ranking for *G. breve*—were used in a multiple curvilinear analysis, with the monthly abundance of *G. breve* as the dependent variable. The salinity, temperature, and abundance ranking of *G. breve* for each month were obtained by computer for all 87 months, using the surface values for stations in north-south areas 0-6, that lie within a band from 4 miles inside of the passes to 15 miles offshore. For the wind variable we used hours per month of wind over 7 kts from sector C (onshore direction). The results of the analysis are shown in Table 3 and Figure 8.

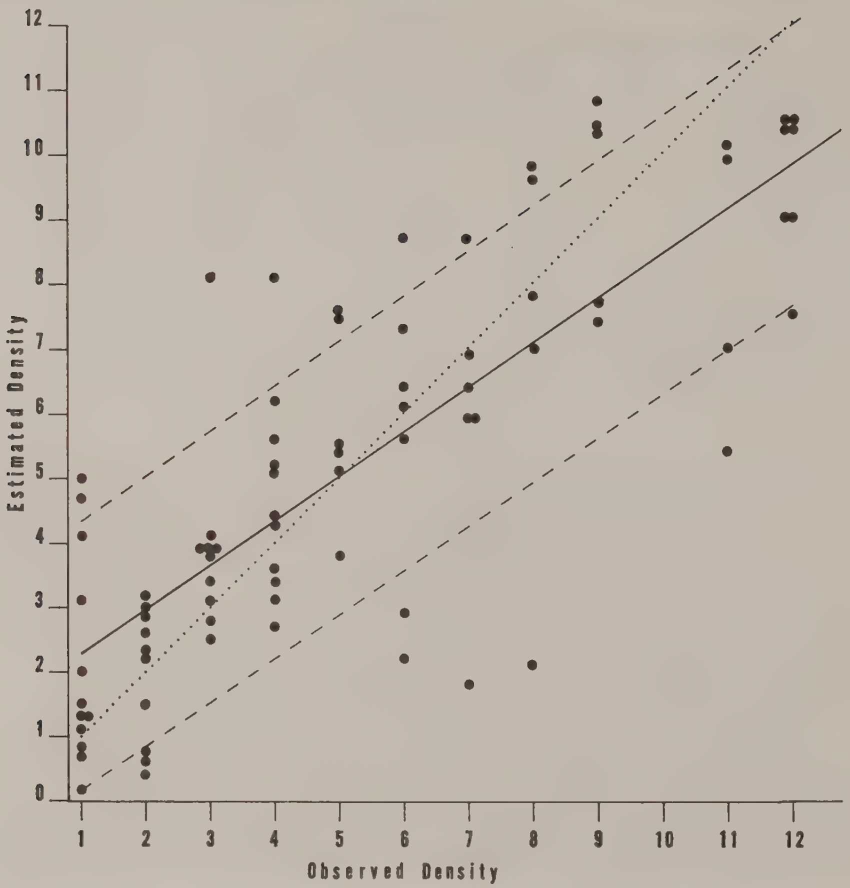

FIGURE 9. Regression of the estimated monthly abundance ranking of *G. breve* on the observed ranking.

The index of multiple correlation, $P_{1.2345}$ for the four independent variables was 0.7817 ± 0.0458. The square of the index, 0.611, indicates that about 61 per cent of the variation in density of red-tide organisms during the period studied can be accounted for by the four independent variables. This value is only slightly more than the variation attributable to the previous month's abundance of organisms, about 57 per cent.

Salinity, temperature, and wind, however, appear to account for about 39 per cent of the variablity. Adding the previous month's density as an additional variable thus added not 57 per cent, but only 18 per cent to the amount of variability accounted for. It will be noted that the standard error of estimate for the four-variable index of correlation (despite the loss of several degrees of freedom for curvilinearity) was about 8 per cent less. Thus it would appear that there is considerable interaction between the previous month's abundance and the remaining independent variables.

Results of the analysis are depicted as a nomograph in Figure 8. The use of the nomograph is relatively simple. Where the abundance ranking the previous month (top diagram) intersects the curve, the abundance ranking is read from the left-hand scale. This ranking is now corrected successively by the values of each of the three remaining variables. In using these three corrections it would be hazardous to attempt a correction beyond the range of values given. The correction curves of Figure 8 for temperature and salinity appear to be more or less mirror images. This relation was suggested by Figure 6, which shows that blooms tend to occur at lower salinities when the temperature is high, and vice versa.

The predictive value of the data is rather low. The relation between the observed density rankings of *G. breve* and the rankings estimated from the multiple correlation analysis (Fig. 8) is shown in Figure 9. With about 40 per cent of the variablity unaccounted for, the points are widely scattered. The slope of the regression line is less than that of the one-to-one slope (dotted line), so that all of the heavy blooms (11 and 12 rankings) are underestimated. Undoubtedly a portion of the variability unaccounted for is caused by variability in the adequacy of sampling throughout the period. There is also a strong implication, however, that much of the remaining variability is caused by one or more additional factors.

Effects of Chemical Factors

In the introduction of this report, nine chemical determinations are listed that were made over varying periods of time for samples collected simultaneously with samples of *G. breve*. Plotting of monthly means of each of these chemical determinations against the residuals of the abundance ranking of *G. breve* from the multiple correlation analysis clearly shows no indication of association for inorganic PO_4-P, copper, alkalinity, ammonia NH_3-N, or total organic nitrogen. The data on total organic nitrogen included only seven months, so no result could have been expected.

We determined the correlation of each of the remaining four variables with the above-mentioned residuals (Table 4). As should be expected, plots of these variables against actual abundance ranking of *G. breve* rather than against the residuals showed less correlation. For inorganic nitrogen the plots indicated a somewhat curvilinear relationship which a logarithmic transformation appeared to make linear.

None of the chemical determinations show a statistically significant correlation with the residuals. The negative correlation with silicon,

−0.48, is very close to being significant. Samples over a longer period of time are needed to determine whether this fairly high negative correlation is or is not significant.

RELATION OF SALINITY TO RIVER DISCHARGE

Salinity variations are of considerable interest, not only because of the effect of salinity itself on the physiology of *G. breve,* but also because the salinity level gives some indication of the degree of admixture of Gulf of Mexico water with runoff from the land. Since some workers believe that overblooming of *G. breve* is dependent upon some substance or substances that is contained in the runoff, we have examined the relation between discharge and salinity. Monthly discharge in acre-feet was used for the Alafia, Hillsborough, Little Manatee, and Manatee rivers. The salinity data are monthly means of surface samples from areas 0-2, in the band extending from 4 miles inside of the passes to 15 miles offshore. The plots of grouped averages (not shown here) disclosed that the relation between discharge and salinity was curvilinear, but a log transformation of the discharge data appears to be linear when plotted against salinity.

The average monthly salinity is affected by both river discharge and prevailing salinity during the previous month, but these two variables are correlated with each other. Therefore a multiple linear correlation was determined for the 72-month period from May 1955 through April 1961.

Y = mean monthly salinity
X_1 = mean monthly salinity during the previous month
X_2 = log total monthly acre-feet of discharge (−000)
$r_{1.2} = 0.776$ $r_{y_1} = 0.908$ $r_{y_2} = -0.770$
$R^2 = 0.833$ $R = 0.913$
$B_{y_{1.2}} = 0.779$ $B_{y_{2.1}} = -0.166$
$\bar{Y} = 8.373 + 0.784X_1 - 0.668X_2$
$\bar{y} = 33.419$ $\bar{x}_1 = 33.413$ $\bar{x}_2 = 1.724$
$S_{y_{1.2}} = 0.770$

Since 83 per cent (R^2) of the variability in salinity can be accounted for by the two independent variables, it becomes possible to predict salinity, in the area described, a month in advance with a fair degree of accuracy. The degree of accuracy could be improved somewhat if the elapsed time between sampling were reduced.

TABLE 4

CORRELATIONS OF RESIDUALS FROM MULTIPLE CORRELATION OF ORGANISMS WITH FOUR FACTORS VERSUS CERTAIN CHEMICAL DETERMINATIONS

Chemical determination	Monthly means N	Correlation coefficient	P at 0.05	Standard error of estimate of residuals
Calcium	14	0.1465	0.532	3.11
Silicon	14	−0.4836	0.532	2.75
Total phosphorus	59	−0.2216	0.250	2.19
Log of NO_3-NO_2-N	53	−0.2126	0.273	2.29

DISCUSSION

The analysis of published data from 7½ years shows clearly that the abundance of *G. breve* depends upon several factors. All three of the chief environmental factors studied—salinity, temperature, and wind—show a curvilinear relation to *G. breve* abundance.

Temperature and salinity appear to interact so that lower temperatures are less unfavorable at higher salinities and vice versa. We agree with the statement of Dragovich & May (1961) that, "The distribution of *G. breve* seems to be restricted by temperature minima rather than maxima." There is also a salinity range favorable to blooms of *G. breve*. Medium to heavy blooms occurred only in months with average salinities between 28.9‰ and 34.6‰. Heavy blooms (11 to 12 rank) occurred in the range from 30.7‰ to 34.0‰. The medium bloom (rank 8) which occurred at a salinity of 34.6‰, and a monthly mean temperature of 17.5°C, illustrates the tendency toward inverse interaction of these two variables.

The effect of wind on abundance levels is of considerable interest. Although wind may not have any direct bearing on multiplication of *G. breve,* it may aid in concentrating them in convergences set up parallel to the shore by onshore winds. Ryther (1955) stated for instance, "Thus there is no necessity to postulate obscure factors which would account for a prodigious growth of dinoflagellates to explain red water. It is necessary only to have conditions favoring the growth and dominance of a moderately large population of a given species, and the proper hydrographic and meteorological conditions to permit the accumulation of organisms at the surface and to effect their further concentration in localized areas."

Many marine biologists have commented that dinoflagellates tend to multiply after the diatom blooms are over, and nutrients are low. To accomplish this the dinoflagellates must be able to concentrate substances from a large volume of water. It has been hypothesized that this concentration might be accomplished through two circumstances; first the motility of the organism, second through the vertical currents set up by convergences. Thus slow-moving, downward currents, combined with motility of the organism, should favor multiplication. The situation would become unfavorable, however, if stronger winds increased the speed of the downward currents to such an extent that the organism could no longer maintain itself at the surface. The shape of the correction curve for hours of onshore wind (bottom diagram in Fig. 8) appears to substantiate this hypothesis. The most favorable area of the curve ranges from about 30 to 80 hr per month of onshore winds about 7 kts. The curve falls off steeply below 25 hr and gradually above 80 hr; the maximum negative effect is at about 170 hr and beyond.

It is of interest to note that the observed correlations of both total phosphorus and the logarithm of nitrate-nitrites with *G. breve* abundance, although too low to be statistically significant, were negative. This finding coincides with the generally expressed opinion that dinoflagellates tend to bloom in waters low in phosphates and nitrates. Although hinted at, the hypothesis cannot be stated as proven by the existing data. On the other hand, the data disagree with the older concept that abundance of the classical nutrients is needed to foster a bloom of dinoflagellates. This view is well expressed by Bein (1957) who, after examination of data on phosphorus samples both within and without red-tide areas, stated, "It is possible that the threshold level of total phosphorus necessary to support dense populations of this organism is lower than originally assumed. The fact that the waters under consideration are usually rich in this mineral has perhaps led to much of the confusion in dealing with this problem. It seems very probable that, insofar as phosphorus is concerned, the areas of the west coast of Florida which have recorded red tides are, at all times, capable of supporting an outbreak."

Even after identification of several of the major factors associated with the variations in abundance levels of *G. breve,* a question remains. Is it likely that further research will result in the derivation of a formula for predicting red tides within a range sufficiently narrow to be more useful than the one presented here? This question is difficult to answer with any assurance. It may be possible to determine with some accuracy the nutritive requirements of *G. breve,* but the practical use of such information may pose problems. Unpredictable variation in any one of the four major factors already considered can easily obscure the relation with one or more additional variables. In fact, to assess the effect of a new factor properly, simultaneous measurements of the four variables already considered would be required. Furthermore, data might be required over a long period of time to establish the significance of the low order of correlation that could be expected.

These requirements of time and simultaneous measurement (coupled with the demonstrated need for fairly extensive sampling to determine the abundance level of *G. breve*) suggest that the task of adding further to the accuracy of prediction would be a long and expensive undertaking. It would scarcely be worth undertaking without prior, exacting information on nutritional requirements, coupled with at least some information on how the substances in question are quantitatively distributed in time and space.

The possible effect of metabolites of other constituents of the plankton on the survival and multiplications of *G. breve* is another aspect of the problem. Evaluation of the effect of such metabolites would be subject to all of the above-mentioned sampling requirements plus the need to measure quantitatively either the metabolites or the plankton from which they are derived.

SUMARIO

CORRELACIÓN ENTRE FACTORES OCEANOGRÁFICOS Y LA ABUNDANCIA DE MAREA ROJA (*Gymnodinium breve* DAVIS) DURANTE 1954-1961

Datos publicados sobre la abundancia del organismo de la marea roja de la Florida, *Gymnodinium breve* Davis, un dinoflagelado desnudo, en el período de Febrero de 1954 hasta Julio 1961, junto con observaciones oceanográficas concomitantes, estuvieron disponibles para su análisis. Este organismo tóxico se presenta esporádicamente en concentraciones mortales para peces, a lo largo de la costa occidental de la Florida entre Cayo Anclote y Cabo Romano, normalmente logrando abundancia sólo dentro de una estrecha banda costera desde 4 millas dentro de los pasadizos hasta 15 millas fuera de la costa.

Los conteos de *G. breve* varían desde 0 a 16,000 por ml y aun una transformación logarítimica permitió una distribución altamente oblícua, de modo que fué necesario utilizar un grado de abundancia (columna 1, tabla 1) para análisis de correlación con factores ambientales.

Se hizo un análisis de correlación curvilínea múltiple, por los métodos de Ezekiel (1941) de aproximaciones sucesivas, entre este grado de abundancia de *G. breve* como la variable dependiente, y cuatro variables independientes: salinidad, temperatura, horas mensuales de vientos hacia la costa de más de 7 nudos y el grado de abundancia de *G. breve* el mes anterior. El índice de correlación múltiple, $P_{1.2345}$ para estas cuatro variables independientes fué 0.7817 ± 0.0458; contando así un 61 por ciento, 0.78^2 de variación en la abundancia de *G. breve*.

Los residuales del grado de abundancia de *G. breve* del análisis de correlación múltiple fueron correlacionados con varias determinaciones químicas hechas simultáneamente con el conteo de *G. breve*. No se encontró asociación con PO_4-P inorgánico, cobre, alcalinidad, amonia NH_3-N, o nitrógeno orgánico total. Se encontraron correlaciones de bajo

orden, no a la altura de significación estadística (Vea tabla 4) entre el grado de abundancia y el calcio, silicón, fósforo total y NO_3-NO_2-N. Debe notarse que las correlaciones de bajo orden entre la abundancia de *G. breve* y ambos, fósforo total y NO_3-NO_2-N, fueron negativas. Aunque no de significación, estas correlaciones negatives parecen apoyar el punto de vista de que *G. breve* tiende a florecer a niveles muy bajos de los nutrientes clásicos.

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(O15) ● J. F. T. SAUR (U. S. Bureau of Commercial Fisheries Biological Lab., Stanford, Calif.), *Seasonal Cycle of Sea Level Difference between the Hawaiian Islands and the California Coast.* Time series of the difference in monthly mean sea level have been tabulated for two pairs of stations: Honolulu-San Francisco (1905–1962) and Hilo-Avila (1947–1962). The mean seasonal cycle for Honolulu-San Francisco is asymmetric and has an amplitude of 12 cm. The values are high (66–69 cm) from April through October and low (57–60 cm) from December through February. The Hilo-Avila cycle is similar. When the sea level differences are used to compute geostrophic current, the surface flow is southward throughout the year. It is stronger from the upwelling season through late summer and is weaker in winter, when the occurrence of a north-flowing Davidson Current close to the California coast would decrease the net southward flow. Month-by-month differences suggest that the flow may fluctuate by a factor of 2. A weak flow is indicated for the winters of 1940–1941 and 1957–1958, when the temperatures were well above normal along the California coast, and an El Niño occurred in the eastern tropical Pacific Ocean. Time series of sea level difference between selected pairs of stations may, thus, help to identify anomalous oceanographic periods and to establish the changes in physical conditions and circulation.

Reprinted from Transactions, American
Geophysical Union, vol. 47, no. 1, p. 111.

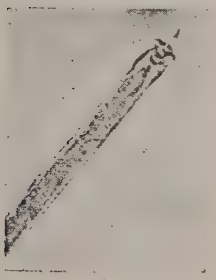
83. Observations on the taxonomic status of amoeboid organisms from the American oyster, *Crassostrea virginica*. THOMAS K. SAWYER, Bureau of Commercial Fisheries, U. S. Department of the Interior, Oxford, Md. (Sponsored by Dr. Carlton Herman)

The American oyster has been recognized as a habitat for inquilinic amoebae as *Amoeba radiosa, Vahlkampfia calkensi*, and *V. patuxent*, and as a natural host for several parasitic amoeboid organisms of uncertain identity. Without exception, the taxonomic status of each recognized species has not been unequivocally resolved. *Amoeba radiosa* was reported by Bovee to be an invalid species designation since many well-known amoebae form a stellate or radiate stage when disturbed. The validity of the two species of *Vahlkampfia* has been questioned by both Hyman and Schaeffer, and Bovee recently placed them in a new genus *Vanella*. The close association of feeding oysters with estuarine and marine plants and protozoans, which themselves may be parasitized by known chytrid fungi and proteomyxans, introduces an additional opportunity for cryptic parasitism in both the oyster and its inquilines. Studies on *C. virginica* from Chesapeake Bay, Md. have revealed 4 different amoeboid organisms of which two show affinities to the Amoebidae and two to the Labyrinthulidae and Vampyrellidae. Microscopic studies of trophozoites, cysts, flagellate swarm cells, and zoospores suggest that at present all amoeboid organisms reported previously from *C. virginica* are of uncertain taxonomic status. The growth of these organisms with *in vitro* methods is presently under investigation and attempts are being made to clarify their life cycles and to establish their taxonomic position within the Sarcodina.

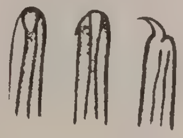
Journal of Protozoology, vol. 13, no. 3 (supplement), p. 23, 1966

Differentiation of Canine Microfilariae with Brilliant Cresyl Blue

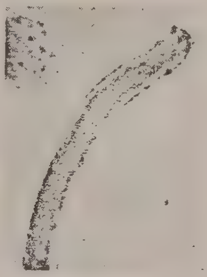
It has been shown that by staining with brilliant cresyl blue, the microfilaria of *Dipetalonema reconditum* (A and B) has a characteristic cephalic hook, whereas that of *Dirofilaria immitis* (C and D) does not. Routine fixing and staining methods often obscure this feature. The R cells and excretory cells (E) of both species stain more distinctly with brilliant cresyl blue than with Giemsa's stain. Differentiating cephalic structures in these species were reported as long ago as 1913 (F. Fulleborn: *Die Filarien des Menschen. Handb. Path. Mikroorganism (Kolle u Wassermann), 2, Aufl. v. 8, (1913): 185-344).*



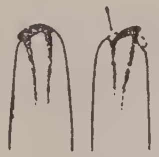
A



B



C



D

E

To demonstrate cephalic structures by using brilliant cresyl blue, thick blood films (blood collected from an ear vein) are stored overnight at room temperature, then dehemoglobinized with tap water or saline solution for 10 minutes. Without drying, the blood films then are transferred to a 1:50 dilution of 1% brilliant cresyl blue, rinsed twice in saline solution and mounted in saline solution, protected with a coverslip, and sealed with melted petroleum jelly-paraffin. Cephalic structures may then be observed on examination with both high-dry, and oil-immersion objectives.—*T. K. Sawyer et al., Proc. Helminth. Soc. of Washington, 32, (Jan., 1965): 15.*

Reprinted from Proceedings, Symposium on Estuarine Ecology, Coastal Waters of North Carolina, Water Resources Research Institute, Raleigh, N.C., May 12, 1966.

INTERESTS OF THE RADIOBIOLOGICAL LABORATORY IN ESTUARINE ECOLOGY

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This paper is divided into three parts: general discussion of rationale and needs, current research activities of the Radiobiological Laboratory, and importance of coordinated research efforts.

Rationale and Needs

It is generally acknowledged that estuaries are important areas for the production of marine organisms -- both from the standpoint of resident populations and of "nursery grounds" for migratory species. The fact that many estuarine organisms are havested commercially in itself justifies the study of the estuaries.

The estuarine ecosystem is highly complex because of variable and transitory populations, tidal movements and currents, tidal and seasonal changes in salinity, and tidal and seasonal temperature fluctuations in northern and temperate latitudes. The variable physical factors make relationships between environmental variables and biological phenomena extremely complex for resident populations and even more complex for migratory or temporary populations.

This complexity -- resulting from a variable species composition and a variable environment -- renders the study of estuaries difficult, especially if the study attempts to encompass large portions of the system. Few investigators or laboratories have the financial and personnel resources needed for research that involves collection, identification, and enumeration of even a moderate number of the species. If physical and chemical factors and research on population dynamics are included, the problem clearly becomes too large to be undertaken by any existing laboratory.

Necessity, therefore, has dictated that the scope of all studies be limited. One approach was to limit the number of organisms studies to one or several closely related species. This autecological approach calls for gathering as much pertinent data as possible on a particular species. It remains extremely useful, especially for species of commercial importance, and it is necessary also for an intelligent assessment of any population of interest.

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[1] The Radiobiological Laboratory is jointly supported by the U. S. Fish and Wildlife Service and the U. S. Atomic Energy Commission.

Unfortunately, autecological studies generally yield data that describe but do not reveal causative or dynamic relationships between the species and environment. The restriction of the scope of the problem precludes making measurements needed to determine causative factors. A broader approach, therefore, is needed. The wider scope can be attained by studying the biological components of the environment on the basis of energy flow. Such an approach does not eliminate studies of single species or the need to know what species are in the biological complex under study. The description of energy flow in an ecosystem requires investigation of interrelationships of physical, chemical, and biological components.

The amount of energy flow through an ecosystem depends on the sunlight energy fixed in photosynthetic producer organisms; all other organisms, therefore, ultimately depend on this source for food (Fig. 1). It follows then that the production of any species or population will be related to and limited by the photosynthetic fixation of carbon by primary producers. The flow of energy in an estuarine ecosystem is not through a food chain, consisting of producers, herbivores, and carnivores, but through a food web. Although the base of the food web is the producers, many aquatic organisms are euryphagous, not simply herbivores or carnivores. Aquatic organisms have diverse food sources (Fig. 1). For example, in an estuarine ecosystem, filter feeders might consume phytoplankton, particulate detritus, and decomposers -- either bacteria or fungi. Other organisms might consume algal epiphytes on aquatic phanerogams. There are two main paths for energy flow from producers to herbivores: the direct path and the path through decomposers or plant detritus or both (Fig. 1). Most grazing and filter-feeding animals are also partly carnivorous because they consume other animals while feeding on plant material. Finally, the complexity of the food web is evident even for a simplified scheme such as that shown in figure 1 if we consider that every population in the environment has feedback of energy in the form of waste products and dead organisms to decomposers and detritus.

It has been shown recently that significant quantities of energy fixed by photosynthetic organisms may be channeled through detritus and decomposers before becoming available to consumer organisms. A decomposer link in the food webs in estuaries was obvious when it was pointed out by Eugene Odum and his students that not much marsh grass was consumed "on the stalk" (Odum, 1961). The inference follows that decomposers which reduce Spartina to detritus also serve as food for heterotrophs. In estuaries, such as those in North Carolina, the role of Spartina, decomposers, and detritus must not be overlooked because these items may be the largest energy source for many organisms. Data on energy flow in a salt marsh in Georgia show that a large amount of production is exported from the marsh into the water (Table 1).

Energy relationships within the estuarine ecosystem provide a framework for comparison and for evaluation of potential biological resources and yield insight into functional relationships within the system. Listed below are some of the processes that need to be studied and some of the applications of the studies:

1. To assess the productive potential of estuaries, we need to measure the basic (primary) productivity including absolute quantities and environmental

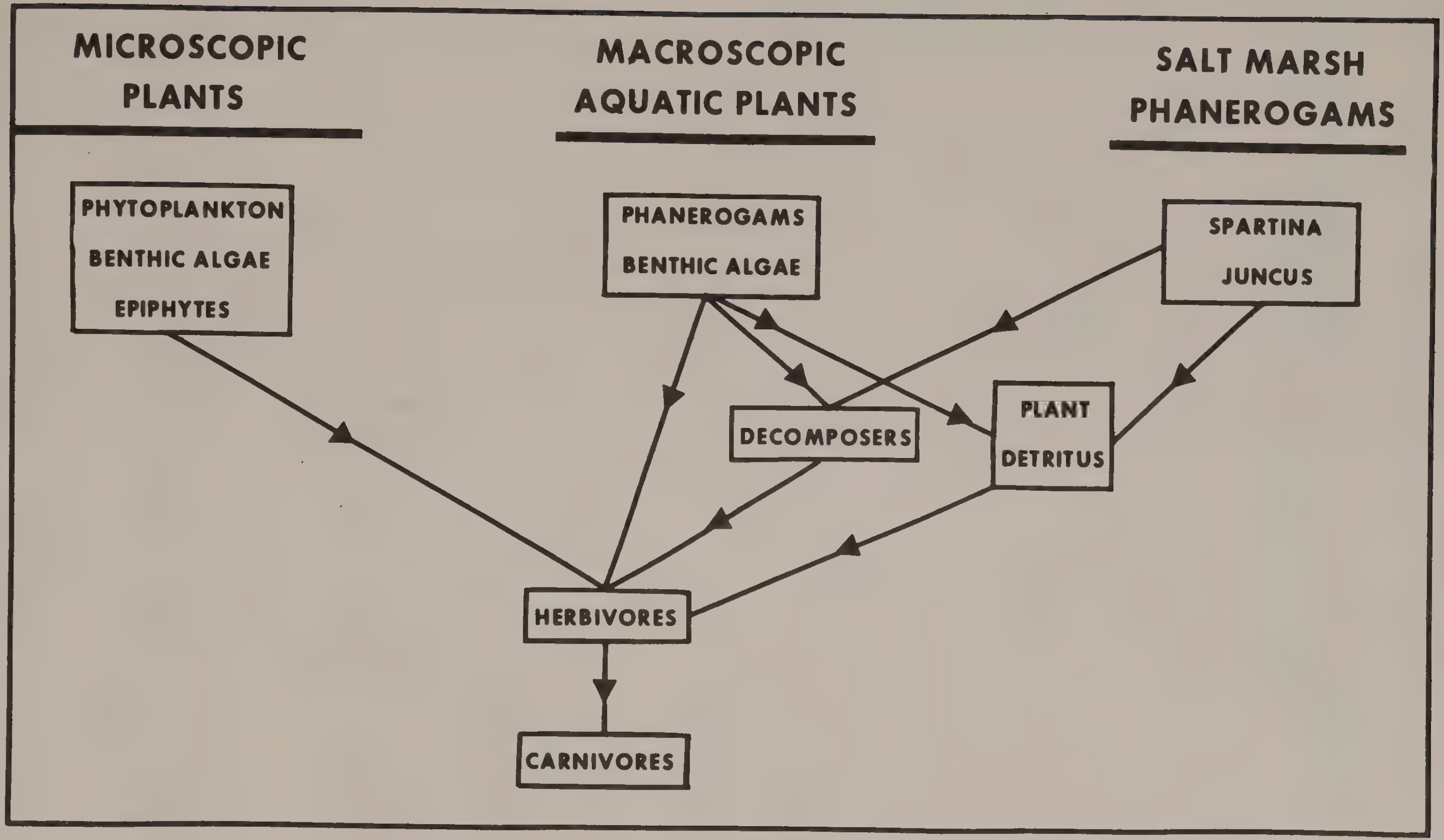
MICROSCOPIC PLANTS
MACROSCOPIC AQUATIC PLANTS
SALT MARSH PHANEROGAMS
PHYTOPLANKTON
BENTHIC ALGAE
EPIPHYTES
PHANEROGAMS
BENTHIC ALGAE
SPARTINA
JUNCUS
DECOMPOSERS
PLANT DETRITUS
HERBIVORES
CARNIVORES

Figure 1. Simplified scheme to show different paths for flow of energy from primary producers to herbivores in an estuarine ecosystem.

TABLE I

Annual Energy Flow In a Salt Marsh Ecosystem*

(Values in kcal/m^2)

	Gross photosynthesis	Production	Respiration
Spartina	34,580	6,585	27,995
Algae	1,800	1,620	180
		8,205	
Bacteria			3,890
Insects		305	224
Spiders		28	5
Crabs		462	372
Mud crabs		31	25
Recycled		123	--
		949	4,516
	Net export - - - - - - - - - -		3,671

* Data from Teal, 1962.

factors such as nutrients, turbidity, temperature, and light that control the process.

2. To apply knowledge of energy flow, we need to investigate food relationships, food habits, food requirements, feeding rates, and availability of food for various stages in the life cycles of commercially important species and for other species which contribute significantly to production in the system. Non-commerical species may be sources of food for commercial species or may be competitors or predators.

3. To understand energy flow, we need to make a thorough investigation of the roles of detritus and decomposers in the economy of the estuarine system.

4. To evaluate management of commercial species in an ecosystem, we need to estimate: (a) the basic productivity (energy flow) being realized as yield, and (b) the maximum yield obtainable by management.

5. Ultimately, for management, we need to know: (a) the desirable species and how their stocks can be controlled to permit maximum flow of energy into desirable species.

Continued research to obtain this type of information should gradually yield increasingly sophisticated methods for managing fishery resources to obtain maximum yields. It should provide a basis for habitat improvement, control of species, selective breeding, and stocking of desirable species. Ultimately, it should provide the capability for prediction and manipulation. As will be pointed out later, these goals are not restricted to the interests of the commercial fisheries. In fact, they should be helpful in establishing guidelines for multiple use that is so important in the utilization of estuaries, and as other natural resources.

Finally, shallow estuaries are highly productive ecosystems (Schelske and Odum, 1962) obviously different from the open ocean and in some ways more complex. The food chain or food web in the open sea is based on one group of primary producers, the phytoplankton, because insufficient light reaches the bottom to support benthic algae. Shallow estuaries have primary producers in the water (phytoplankton), on the sediment (benthic agae, phanerogams, and algal epiphytes), and in the salt marsh (phanerogams). Each group may support separate groups of grazing organisms. In the open ocean the depth of water reduces exchange of dissolved materials between water and sediment to the point that they can be disregarded in predicting the rates, routes, and reservoirs of nutrients. In shallow estuaries, on the other hand, exchange of nutrients between sediment and water may control the ultimate distribution of nutrients. The study of the biology for the estuarine ecosystem differs from that of the open sea.

Research at the Radiobiological Laboratory

The interest of the Radiobiological Laboratory in estuarine research stems from our original mission to study the uptake, accumulation, and retention of radionucludes by fish and shellfish. Although laboratory studies

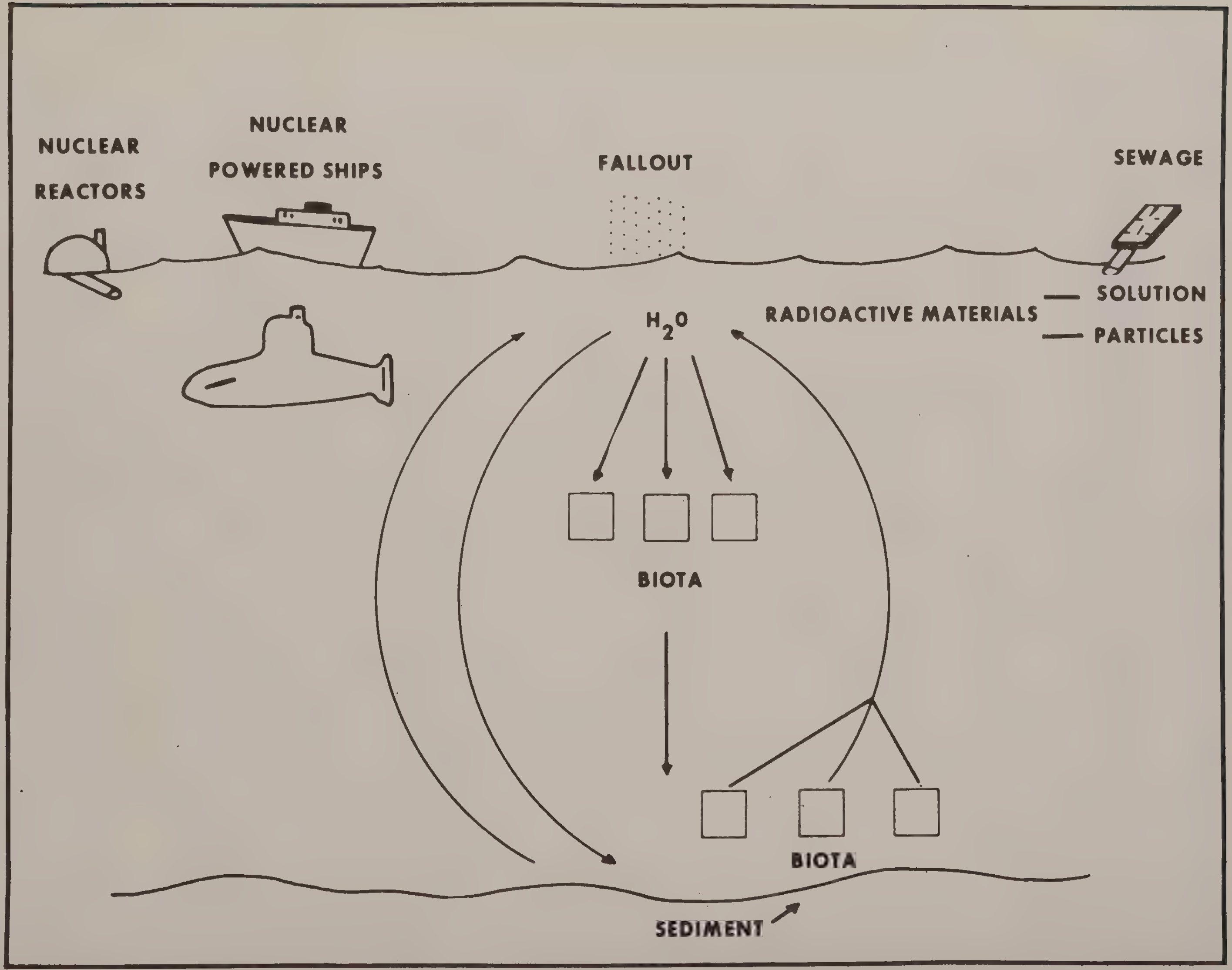
NUCLEAR
REACTORS
NUCLEAR
POWERED SHIPS
FALLOUT
SEWAGE
H_2O
RADIOACTIVE MATERIALS
SOLUTION
PARTICLES
BIOTA
BIOTA
SEDIMENT

Figure 2. Cycling of radioactivity in an estuary.

serve as one means of collecting data, experiments in ponds and estuaries and knowledge of the environment are needed to fulfill our ultimate objective -- prediction of the fate and effect of radioactivity introduced into an estuary (Rice, 1965a). Research within our laboratory is organized around these objectives and the development of radioisotope techniques for fishery research (Rice, 1965b). Definition of the rates, routes, and reservoirs of radioactivity is a basic ecological problem (Fig. 2). The dynamics of an ecosystem can be reduced to two basic processes: flow of energy and cycle of materials. Some of our research is concerned with the cycle of radioactive materials and some with the flow of energy which drives the movement of materials.

Three of our four research programs -- estuarine ecology, biogeochemistry, and pollution studies -- are concerned with the fate of radioactivity in the biotic and abiotic components of the environment. The fourth research program is concerned with the effects of radiation on marine organisms.

Estuarine Ecology Program: The biological productivity of estuaries and the distribution of fallout radioactivity in estuarine organisms are being investigated. To date, the flow of energy through phytoplankton has been studied (Williams and Murdoch, 1966; Williams, in press). At present, the flow of energy through salt marsh phanerogams is being investigated. Work on benthic algae is planned in the future. These studies will provide data for estimating the productive potential of estuaries near Beaufort, North Carolina.

Fallout radioactivity in estuarine organisms is being measured to provide a reference line for environmental radioactivity and to determine biological indicators of radioactivity in estuaries. Biological indicators are defined as organisms that accumulate relatively large amounts of radioactivity from the environment. In addition to the measurement of fallout in biological indicators, the mechanisms of accumulation or the cycle of the radioisotopes have been studied (Schelske. 1966).

Biogeochemistry Program: Rapid accumulation of radioisotopes by marine organisms suggests that active ion transport supplies some metabolic mineral requirements. The mechanisms of ion transport through cell membranes are being studied and the distribution and metabolic functions of stable and radioactive ions within the cells of certain estuarine organisms are being determined (Gutknecht, 1965).

We know, for example, that the oyster concentrates several elements to levels many times those in sea water. We have studied the rates of uptake and loss of some of these elements with radioisotopes and are now concerned with the metabolic routes and reservoirs within the organism. We are therefore studying the interactions of proteins with trace metals and the relationships of trace metals to certain enzymatic activities.

Estuarine organisms and sediments must also be characterized chemically before we can draw conclusions on accumulation or exchange of nutrients and radioisotopes. Environmental samples collected for radioassay are also analyzed for trace metals by atomic absorption spectrophotometry, so that we can correlate the cycling of trace elements and their radionuclides in the estuarine environment with chemical composition.

Pollution Studies Program: We are exploring the routes and rates by which radioactivity released into the estuarine environment might pass through the food chain to man (Duke, Baptist, and Hoss, 1965). The scope of research ranges from experiments in the natural environment with communities of organisms to those conducted in the laboratory with single species of organisms maintained in small volumes of water.

Observations are made on the cycling of radionuclides released in artificial tidal ponds to compare the rates of accumulation by different species of organisms under the same environmental conditions (Duke, Willis, and Price, 1966). The rates should approximate those which occur in nature since the physiological condition of the organisms is not affected as much as in laboratory experiments. Samples of the biota, sediment, and water are removed from the pond periodically, and analyzed for radioactivity. Living organisms are analyzed and returned to the pond so the numbers of organisms will be constant throughout the experiment.

All processes that occur in an estuary cannot be studied in situ; therefore, experiments are conducted also under controlled conditions in the laboratory. For example, the interaction of environmental factors such as pH, temperature salinity, and concentrations of stable elements on the exchange of radionuclides, between sediments and sea water and the accumulation of radionuclides by estuarine organisms are being determined by varying one factor while the others are maintained constant. Experiments in the laboratory include studies of the retention of radionuclides by fish (Hoss, 1964; Baptist, 1966) and shellfish (Price, 1965) and the passage of radionuclides from water to phytoplankton to organisms of other trophic levels. Analyses of the related stable-element content of the organisms in each trophic level are made so that the passage of a radionuclide through the food chain can be related to the specific activity of the organisms and their environment.

Radiation Effects: This fourth program is concerned with the effect of ionizing radiation on marine organisms, and is a logical sequel to the investigations of the fate of radioactive materials in the marine environment. The main objectives are to determine the influence of environmental factors on the response of estuarine organisms to ionizing radiation and to characterize the physiological and morphological effects of radiation on these organisms (White, 1964). We are now investigating the influences of temperature, salinity, population density, space, and food on the responses of estuarine organisms to radiation. The interactions of radiation, salinity, and temperature are determined by subjecting various developmental stages of resident estuarine species to combinations of the three factors and measuring changes in LD-50's, growth, and respiration (White and Angelovic, 1966).

The radiation syndrome in marine fish is characterized by changes in the blood, tissues, organs, and membrane permeability. The hematopoietic system is especially sensitive to radiation, and radiation syndromes usually include changes in blood physiology. Changes in the cellular blood components of marine fish that have received lethal and sublethal doses of radiation have been described (Engel, Angelovic, and Davis. 1966). We plan to examine radiation-induced changes in blood including: ionic and osmotic concentrations, electrophoretic patterns of plasma proteins, plasma enzymes, cell volumes, and cell numbers. The order of appearance of radiation effects and the tissues and organs which are most sensitive to radiation will be established. This information can be used for selected indicator organisms to evaluate potential radiation damage to biological resources in areas that might be contaiminated accidentally.

Additional information on research can be found in the Annual Reports[2] of the Radiobiological Laboratory.

Importance of Coordinated Research Efforts

The importance of research on energy flow as it relates to commercial fisheries has been emphasized by the Radiobiological Laboratory. It was pointed out, however, that probably no laboratory is able to make a comprehensive estuarine study. Coordinated research would benefit the interests of the Bureau of Commercial Fisheries, and other Federal and State agencies, universities, and private agencies. It would, for example, be helpful in answering the following questions:

1. What is happening to estuaries? The answer to this question requires an inventory of the present biota and environmental conditions so we can assess past and future changes.

2. What are the consequences of environmental alteration on the value of estuaries? We should know how pollution, dredging, and other man-made changes are affecting the biology and especially the food-producing capabilities of the estuaries and the oceans.

3. What needs to be done to preserve and maintain estuaries? North Carolina estuaries, unlike those in many parts of the United States, have not felt the full impact of man's intervention. It is especially important then to accumulate background information of all types so present conditions can be documented as well as possible.

4. What is the role of estuaries and estuarine organisms in the biology and food production of the sea? Estuaries are nursery grounds for many species that have commercial importance, but it is not known how much the estuary contributes in this manner or how much production is transported to offshore areas where it is harvested as sea food.

5. What needs to be done to study estuaries comprehensively? This is a very important question since upon it hinges the procurement of knowledge that will be needed for future value judgments concerning the preservation

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[2] Annual Reports of the Radiobiological Laboratory are published as Fishery Circulars and can be obtained from the Bureau of Commercial Fisheries, U. S. Fish and Wildlife Service, Washington, D. C.

of estuaries for effective utilization by man. Examples of such value judgments might come in the form of -- How valuable are the commercial fisheries? Or -- What is the recreational value?

At present, coordinated research is mandatory to provide fundamental data as a basis for future decisions about estuaries. These studies would provide the best estimates available to date on biological resources and on potential biological productivity. The biological productivity in the form of food resources has always been important in assessing the dollar value of estuaries and it will likely be even more important as demand increases for food. These investigations also would provide a mechanism to make a large number of related or simultaneous observations which should give us insight into the dynamics of the environment and the best available information on how different processes in the environment are related. The diversity and extent of measurements by different investigators or agencies can provide the basis for many correlations. Thus the work of all concerned will be strengthened. The correlations obtained can and should be studied experimentally to determine if a cause-and-effect relationship exists. Undoubtedly, these experimental studies will provide clues for additional measurements to be made in estuaries to establish further the cause-and-effect relationships.

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The Fate of Fallout Radioactivity in an Estuary

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As uses of nuclear energy increase, amounts of artificially produced radioactivity in the environment possibly may increase also and, eventually radioactivity may be an environmental factor affecting the biota, including man, in many different ways. Organisms have always been exposed to naturally occurring radiation in their environment, primarily from cosmic rays and from K^{40}, Th^{232}, and U^{238}. The latter two radionuclides and their decay products, found in some minerals, cause certain geographic areas to have high levels of environmental radiation. The radionuclides C^{14} and K^{40} occur naturally in all organisms in concentrations proportional to the amounts of stable elements, but neither is present in sufficient concentration to increase environmental radiation significantly. At present, the sources of artificially produced radioactivity are fallout, nuclear reactors, and wastes from industrial, clinical, and research applications. Although present amounts of radioactivity are insufficient to produce noticeable deleterious effects, the significance of possible future increases in the environment should be evaluated.

At the Radiobiological Laboratory this problem is being investigated by studying the fate and effects of radioactivity. The fate is, of course, where the radionuclide goes after it enters the environment, and the effect pertains to how the radiation affects the biota. It should be mentioned that in addition to killing organisms, radiation may sterilize organisms and otherwise affect reproductive potential, may cause genetic mutations, and may cause many subtle changes in different life processes. To determine how radioactivity might affect the biota, the amounts and types, or fate, of radioactivity in organisms and their environment must be known. This discussion is concerned with the fate of fallout radioactivity in the estuarine environment near Beaufort, North Carolina.

What is Radioactivity?

Radioactivity is a property of certain atoms, called radioisotopes or radionuclides, that have unstable nuclei and undergo spontaneous disintegration. The disintegration rate or decay rate of each radioisotope is characterized by a half-life, the time required for half of the atoms to disintegrate. Upon disintegration, energy in the form of ionizing radiations is released from the nucleus. The types of radiations produced are alpha, beta, and gamma. Alpha particles are positively charged particles composed of two neutrons and two protons and are equivalent to the nuclei of helium atoms. Beta particles are either negatively or positively charged electrons. Gamma rays are electromagnetic radiations similar to X rays and ordinary light but usually have higher energies. The particulate alpha and beta radiations have smaller ranges in matter than gamma rays; most beta radiation and all alpha radiation are absorbed by laboratory glassware, whereas some gamma rays will pass through the walls of the laboratory.[1]

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[1] For a non-technical discussion of radioactivity and atomic energy see Craven (1963).

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A large number of the artificially produced radionuclides are non-essential elements for biological processes and consequently may be unfamiliar to biologists (Table 1). Some are fission products formed by the splitting, or fission, of uranium and plutonium atoms. Only a few fission products are listed in Table 1, but as many as 200 different radionuclides may be produced during the fission process. Many will decay quickly because their half-lives are less than a few minutes. In addition, neutron-induced radionuclides are produced during fission by neutrons that bombard and "activate" stable elements.

What is Fallout Radioactivity?

It is the radioactivity that results from a nuclear explosion in the atmosphere and is later deposited on the earth's surface. Fallout is either "local" or "world-wide" (Comar 1963). Local fallout occurs within 24 hours after an explosion that is low enough for large quantities of soil or water to be sucked up into the hot fireball. Local fallout is therefore restricted to the vicinity of an explosion. World-wide fallout, as the name implies, may be deposited anywhere on the earth's surface. This radioactivity may remain in the upper atmosphere for long periods of time and be transported over the world before it becomes fallout. Almost all of the fallout being deposited currently has been in the stratosphere since the last series of large atmospheric tests in 1962.[2]

TABLE 1

Some gamma-emitting radionuclides that might occur in environmental samples. (F. P. denotes fission product, N. I. denotes neutron-induced radionuclide, and N. O. denotes naturally occurring radionuclide.)

Isotope	Source	Half-Life	Gamma Energy (Mev.)
I^{131}	F.P.	8.05 d.	.364*
Ba^{140}-La^{140}	F.P.	12.8 d. -40 hr.	.487*, 1.60*
Ce^{141}	F.P.	32.5 d.	.145
Ru^{103}-Rh^{103}	F.P.	40 d.-57 min.	.498
Zr^{95}-Nb^{95}	F.P.	65 d.-35d.	.77
Zn^{65}	N.I.	245 d.	1.11
Ag^{110}	F.P.	250 d	.68*, .885*
Ce^{144}-Pr^{144}	F.P.	285 d.-17 min.	.134*, .696**
Mn^{54}	N.I.	300 d.	.84
Ru^{106}-Rh^{106}	F.P.	1.0 yr.-30 sec.	.513, .624**
Co^{60}	F.P.	5.27 yr.	1.17, 1.33
Sr^{90}-Y^{90}	F.P.	28 yr.	***
Cs^{137}	F.P.	30 yr.	.662
C^{14}	N.O.	5730 yr.	***
K^{40}	N.O.	1.3×10^{9} yr.	1.46
U^{238}	N.O.	451×10^{9} yr.	****
Th^{232}	N.O.	1.41×10^{10} yr.	****

* Major peak
** Minor peak
*** No gamma radiation
**** Complex decay scheme with a number of daughter radionuclides and many radiations of all types.

How is Fallout Radioactivity Measured?

Even though amounts are small, fallout radioactivity can be measured by using the techniques and equipment described below: (1) Only gamma radioactivity is being measured at our laboratory which simplifies sample preparation because, as mentioned earlier, gamma rays are not absorbed appreciably in matter. (2) Large biological samples, as much as 1.0 kg, are concentrated, usually by dry ashing at 450 C. The radioactivity in the sample is also concentrated by ashing and can be placed in more intimate contact with the detector so more radiations emitted from the sample are absorbed by the detector. (3) A large detector, 4- x 4-inch NaI(T1) scintillation crystal, is used because it absorbs more of the emitted radiations than a smaller detector. (4) Background radiation arising from cosmic rays and other sources is reduced by a large shield (Fig. 1), weighing about 7 tons, constructed of steel plates and lined with lead and stainless steel. The top, bottom, and sides are 6 inches thick. (5) Long counting times, as much as 100 minutes, are used for measurements. Because the recorded counts are cumulative, smaller and smaller amounts of radioactivity can be measured by increas-
established statistically.
ing counting times within limits that can be

Gamma rays emitted by radionuclides have known energies (Table 1). The multichannel analyzer (Fig. 1) used to measure gamma radiation absorbed by the scintillation detector can be calibrated so that each channel measures radiation in a given energy range. The resulting measurement is a gamma ray spectrum in which radioactivity can be determined both quantitatively and

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[2] For non-technical discussion of fallout radioactivity see Comar (1963).

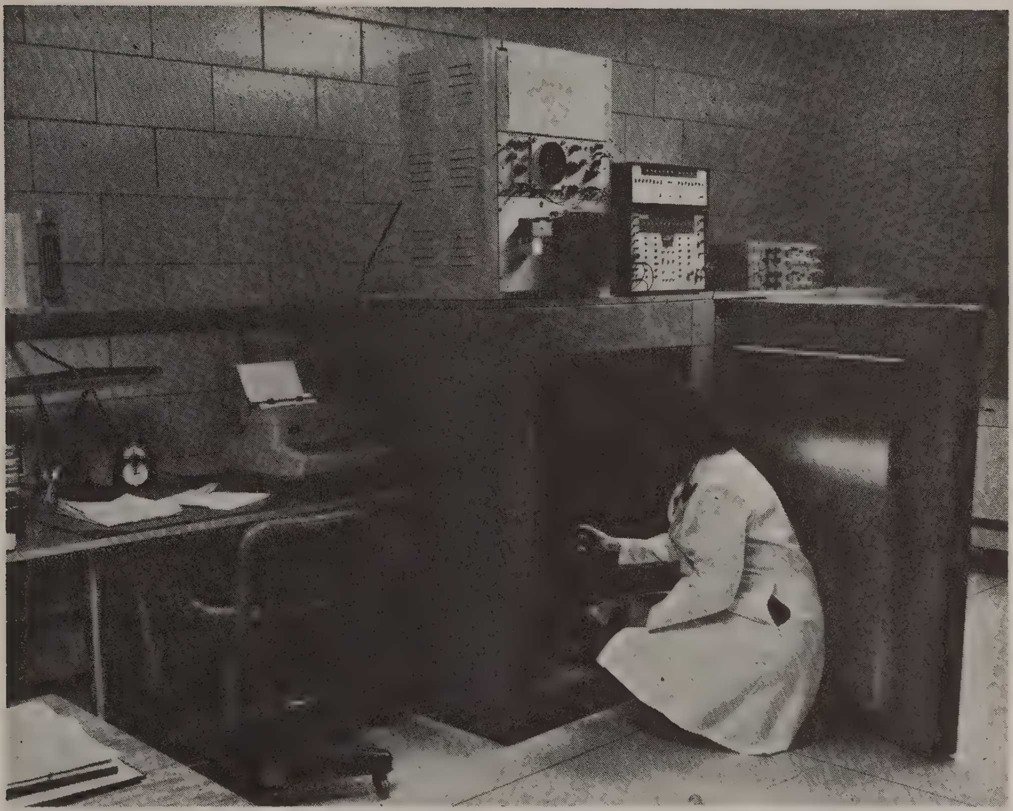

Fig. 1. Low background gamma counting system. Technician is placing sample on the scintillation detector in the 7-ton shield. The multi-channel analyzer and oscilloscope are on top of the shield, the IBM typewriter is on the desk at the left side of the shield.

qualitatively from the number of counts recorded for specific energy levels (Fig. 2). A photopeak of known energy in the spectrum means that the sample contains one or more radionuclides that emit gamma rays corresponding to the photopeak energy in question.[3] The spectrum of gamma radioactivity analyzed with the multichannel analyzer can be seen on the oscilloscope screen or can be printed out, channel by channel, with the IBM typewriter (Fig. 1) and then be plotted (Fig. 2).

The photopeak energy of different gamma rays is obvious in the gamma spectra of different radioisotopes. As examples, the different energies of Mn^{54}, Zn^{65}, and Ce^{144} (Table 1) are evident in their respective gamma spectra (Fig. 2). The three photopeaks are obvious also in a sample containing the three radioisotopes (Fig. 2).

Why Measure Fallout Radioactivity?

At our laboratory there are three purposes for measurements of fallout radioactivity in the estuarine environment: (1) to establish existing levels of radioactivity in estuarine organisms, (2) to determine biological indicators of radioactivity, and (3) to study the pathways by which different organisms accumulate radioactivity.

Knowledge of existing levels of radioactivity in organisms is needed to determine whether or not amounts are changing. Data on amounts in organism also are needed for

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[3] Usually radioisotopes can be identified from photopeaks and half-lives. The half-life can be established by counting the sample at different times. However, a chemical separation can be used if it is needed for verification of the identification.

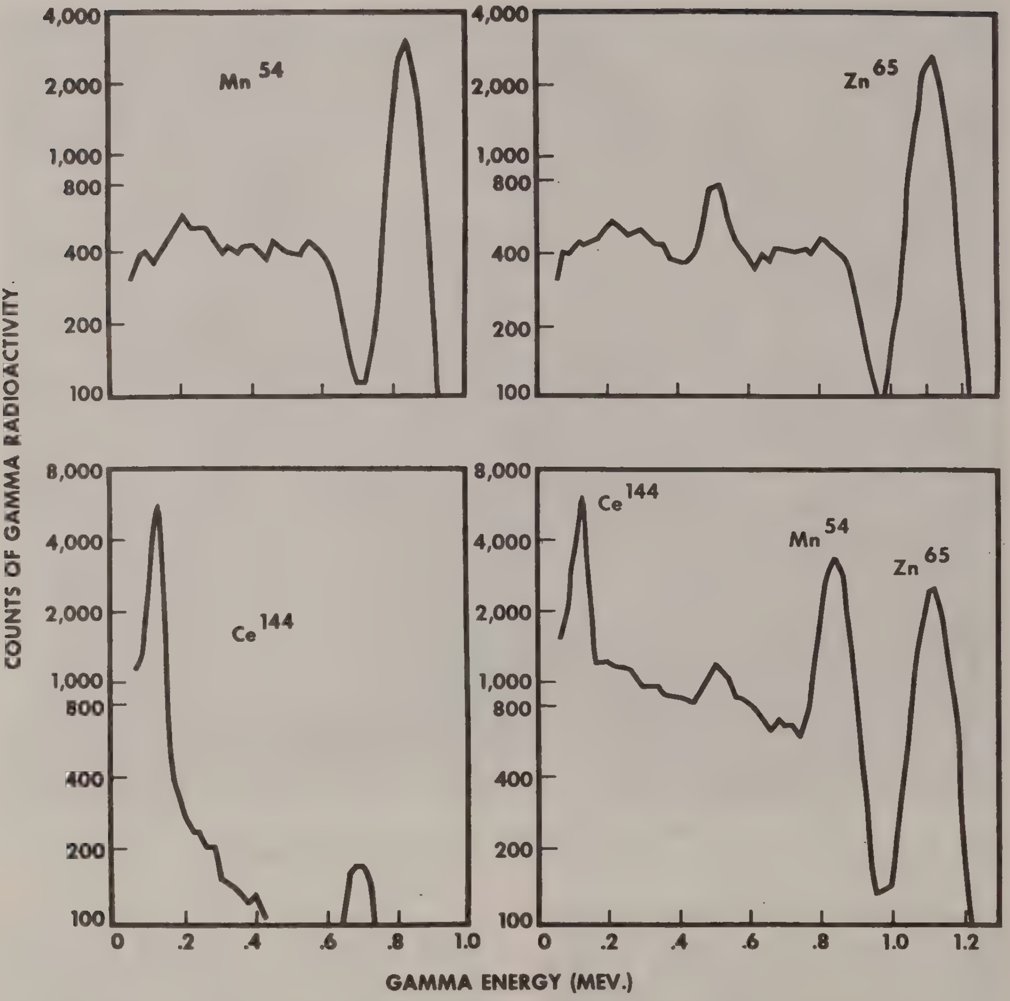

Fig. 2. Individual gamma spectra for Mn^{54}, Zn^{65}, and Ce^{144} and a composite spectrum (lower right) of the three radioisotopes analyzed at the same time. Individual components can be separated by successive "stripping" or subtraction of each spectrum from the composite spectrum. The spectrum with the highest energy (Zn^{65}) is stripped first and then the spectrum with the next highest energy (Mn^{54}) is stripped until the components are resolved. See Fig. 8.

predictions of radiation effects from known or anticipated increases in environmental radioactivity. In other words, how much would radioactivity have to be increased to manifest a particular radiation effect? To have an answer one also must determine experimentally how much radiation is needed to produce the effect in question.

Biological Indicators of Radioactivity

Some plants and animals referred to as biological indicators contain relatively large amounts of one or more radionuclides. To know which organisms are biological indicators is particularly useful in making a survey of environmental radioactivity. In such cases, the only organisms that need to be collected and analyzed are those that are biological indicators for the particular radionuclides of interest. Ideally a biological indicator should be: (1) either sessile or nonmigratory so the site where the radioactivity was accumulated can be located, (2) abundant so sufficient material can be collected, (3) easily collected so minimum effort is expended to obtain large samples, (4) distributed over a wide geographic range so fewer indicator organisms are required to make comparisons between areas, and (5) an indicator for several radionuclides so fewer organisms are needed to determine environmental radioactivity.

To study biological indicators and the mechanisms by which biological indicators accumulate fallout radioactivity is in reality to study the ecology and biology of each species. It is anticipated that fallout radionuclides can be used as tracers for natural processes in the environment in the same way as tracers are used in laboratory experiments. Fallout radionuclides in the environment are accumulated by organisms under natural conditions. Data obtained from measurements of fallout, as is shown later, enable us to ask specific questions about why organisms are biological indicators and how radioactivity moves through the environment. The general processes involved are shown in Fig. 3.

Organisms are biological indicators because they concentrate many elements from the water in which they live. For instance, the concentration of zinc in an oyster may be 50,000 times greater than in sea water. An oyster therefore may contain 50,000 times more radioactive zinc than an equal amount of sea water. Obviously, it would be more difficult to measure fallout radioactivity in sea water. Measurements were made by concentrating the radioactivity in 200-liter samples but the amounts were less than those found in biological indicators.

Of the estuarine animals we have analyzed, lamellibranch mollusks contained the most gamma radioactivity. In particular these are bay scallops, *Aequipecten irradians;* American oysters, *Crassostrea virginica;* hard clams, *Mercenaria mercenaria;* and ribbed mussels, *Modiolus demissus* (Fig. 4). These mollusks not only meet the criteria established previously for biological indicators but also can be collected economically and conveniently (Fig. 5).

Collectively, these mollusks contained all the radionuclides we have found in environmental samples.[4] These radionuclides in the latter part of 1963 were Mn^{54}, Zn^{65}-Ce^{144}, Ru^{106}, Cs^{137}, and Zr^{95}-Nb^{95}. The sediments in or on which the mollusks live, however, contained mostly Ce^{144} and Zr^{95} Nb^{95} (Fig. 6). Samples of cord grass, *Spartina alterniflora* (Fig. 7) that grows extensively in the intertidal zones of the estuary also contained these two radionuclides. Both Ce^{144} and Zr^{95}-Nb^{95} are in the particulate state in sea water; these "sticky" particles apparently were either precipitated or adsorbed onto the sediments and cord grass.

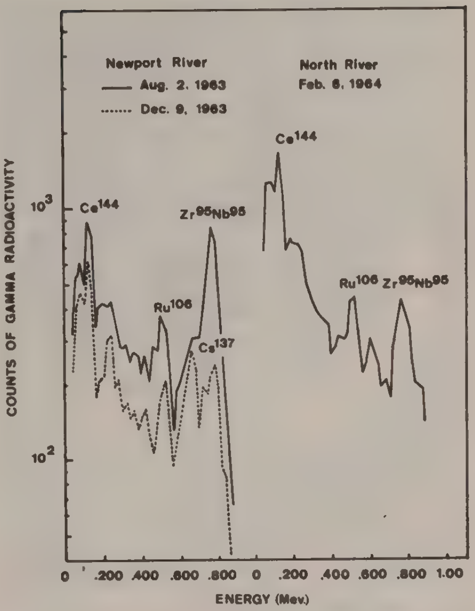

Fig. 3. A schematic diagram showing the processes that dilute or concentrate radioactive materials entering an estuary (From Rice, 1965).

Ecological Significance of Accumulated Radioactivity

The fate of fallout radioactivity entering an estuary is determined by environmental factors (Fig. 3), and by the specific radionuclide. A radionuclide of a non-essential element may not be passed through the food

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[4] Measurements of fallout radioactivity were not started at our laboratory until the fall of 1963. Therefore, we did not find shorter-lived radionuclides that were produced during the nuclear weapons tests in 1962.

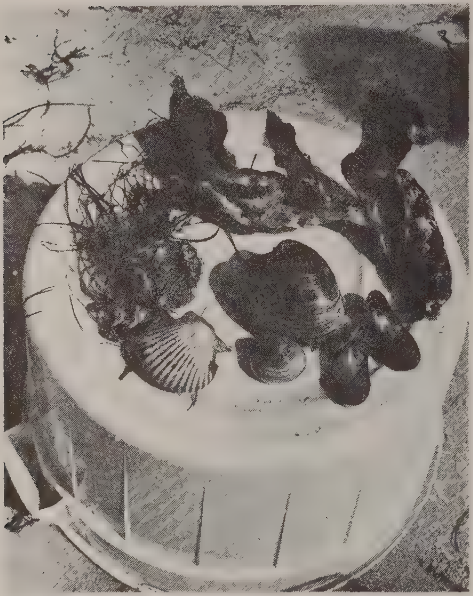


Fig. 4. Lamellibranch mollusks. In the foreground, left to right, are bay scallops, *Aequipecten irradians;* hard clams, *Mercenaria mercenaria;* and ribbed mussels, *Modiolus demissus;* a cluster of American oysters, *Crassostrea virginica* is shown in the background. Bay scallops are found in beds of eel grass, *Zostera marina,* shown near the scallops.

chain because, generally speaking, it will not be accumulated and assimilated by organisms. As examples, Ce^{144} and Zr^{95}-Nb^{95}, present in sediments and cord grass (Figs. 6 and 7), were found in measurable amounts in only a few organisms, whereas Mn^{54} and Zn^{65}, radionuclides of essential elements, were found in many organisms even though Mn^{54} and Zn^{65} represented a small fraction of the total fallout radioactivity. Both accumulated and environmental radioactivity are reduced by decay. Radionuclides with short half-lives may be accumulated and then decay faster than the rate of accumulation. An example is the rapid change in the amounts of Zr^{95}-Nb^{95}, which has a 65-day half-life, in sediments and cord grass (Figs. 6 and 7). The half-life of the radionuclide may also affect the fate because the rate of decay may nearly equal the rate of accumulation so only small amounts of a particular radionuclide are accumulated by an organism.

The gamma radioactivity accumulated by scallops (Fig. 8) was different from that of

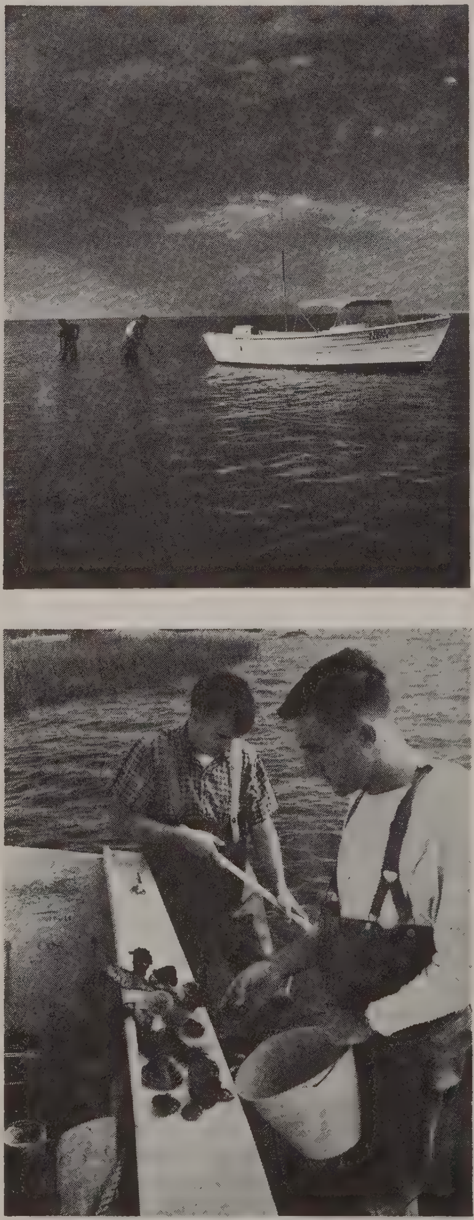
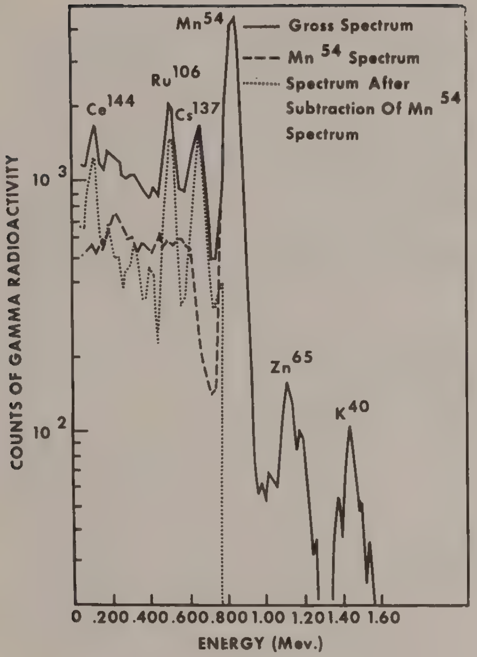


Fig. 5. Biologists collecting samples with rakes in the shallow estuary (above). Animals collected by raking (below) include a purple sea urchin (in the foreground), *Arbacia punctulata,* two white sea urchins, *Lytechinus variegatus,* a colony of tunicates, *Molgula manhattensis,* and clams, oysters, and scallops also shown in Fig. 4.



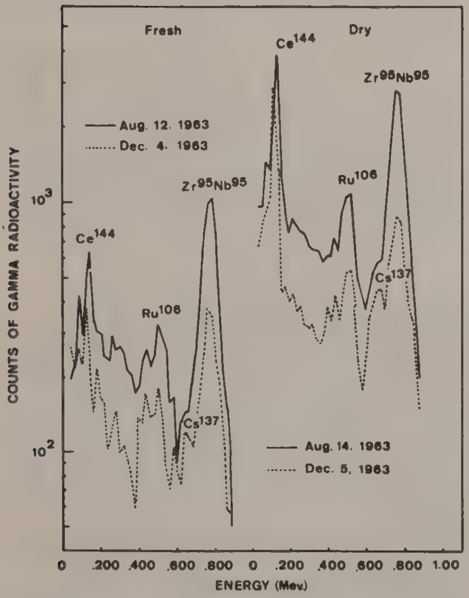


Fig. 7. Spectra of gamma radioactivity in cord grass *Spartina alterniflora. Fresh* represents 1963 growth and *dry* represents 1962 or older growth. Gamma spectra for December are recounts of samples collected in August. The decay of Zr^{95}-Nb^{95} (65-day half-life) is evident in the recounts.

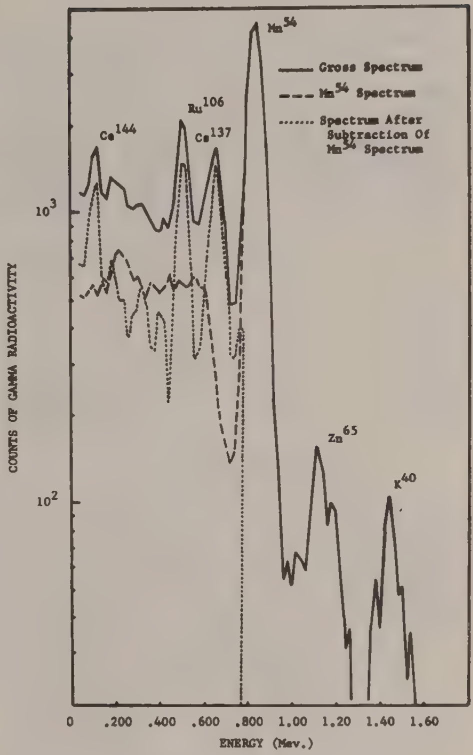


Fig. 8. Spectrum of gamma radioactivity in bay scallops, *Aequipecten irradians.*

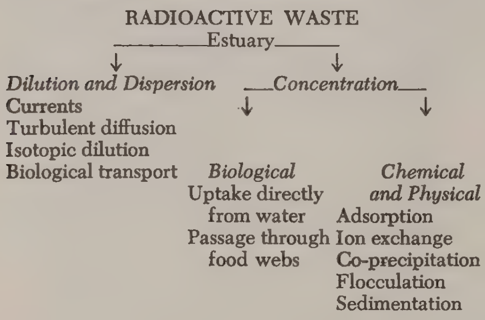
sediments or cord grass (Figs. 6 and 7). Scallops contained more radioactivity than the other mollusks (Schelske, Smith, and Lewis 1965) but the most interesting part of our results was that scallops contained about 40 times more Mn^{54} than either clams or oysters. Clams, oysters, and scallops are filter feeders that occupy the same habitat and each presumably filtered microscopic food materials from the same water. Experiments and measurements were started, therefore, to discover why the scallop accumulated so much Mn^{54}. Some were successful in that we obtained meaningful information, and some apparently yielded no instructive results. Other experiments are still in progress.

The distribution of Mn^{54} and stable manganese were measured in scallop tissues (Table 2). The concentration of Mn^{54} was 100 times greater in the kidney than in any

TABLE 2

Representative values for Mn^{54}, stable manganese, and specific activity of Mn^{54} in scallop tissues. (Concentrations are based on wet weights. One picocurie, ps, is 10^{-12} curies, and is the amount of radioactivity needed to produce 2.22 radioactive disintegrations per minute. Specific activity is the ratio of the amount of radioactivity to the amount of stable element.)

Tissues	Mn^{54} (pc/g)	Mn ($\mu g/g$)	Specific Activity (pc/μg)
Kidney	97	7,100	.014
Muscle	0.83	14	.059
Gills	0.48	49	.0098
Mantle	0.25	4.8	.052



other tissue and the kidney contained about 75% of the total Mn^{54}. The adductor muscle contained about 10% of the Mn^{54}. The latter point is significant because the adductor muscle is the portion of the scallop that is eaten in the United States. Measurements of stable manganese in scallop tissues revealed why the kidney, the smallest tissue, contained most of the Mn^{54} in the scallop—it also contained the largest concentration of stable manganese (Table 2).

Apparently the scallop contained more Mn^{54} because it also contained more stable manganese than clams or oysters. The stable manganese content of scallops was at least 20 times greater than that of clams. A radioisotope and its stable elements are accumulated in proportion to the amounts present because the chemical behavior of each is the same if both are in chemical equilibrium. The different specific activities for scallop tissues (Table 2) indicate that the Mn^{54} accumulated by scallops was not in chemical equilibrium with the stable manganese in the environment. Possibly, large amounts of Mn^{54} were accumulated by scallops because of food chain relationships that are similar to the accumulation of I^{131} in milk. The I^{131} in fallout may be deposited directly on forage crops that are eaten by cows and large amounts may be transferred to the cow's milk (Comar 1963). It is known that fallout is particulate and to a certain extent insoluble in sea water; it is therefore possible that in some way scallops accumulated Mn^{54} that was not in chemical equilibrium with the stable manganese in the environment. One likely way of accumulation is filtering particles containing Mn^{54}.

The results also pose a more basic question. Why do scallops contain so much more manganese than the other mollusks? At least two hypotheses are conceivable. One is that scallops concentrate manganese more efficiently than the other mollusks. Another is that scallops filter food that contains more manganese than the food of the other filter feeders. Selective feeding by filter feeders is well established (Jørgensen 1955). To date neither of these hypotheses can be ruled out. When one can be, our knowledge about mollusks will have been advanced.

It can be seen that the fate of fallout radioactivity in estuaries is determined by biological, chemical, and physical factors. Measuring fallout radioactivity permits evaluation of these factors and provides unique opportunities and methods for studies of the biology and ecology of estuarine organisms.

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A Jar for Culturing Small Pelagic Marine Organisms in Running Water during Shipboard or Laboratory Studies

By

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Some difficulties encountered at sea when incubating pelagic fish eggs and cultivating small marine invertebrates in running water may be overcome by utilizing porous polyethylene filters to replace bottoms in glass jars. The proportionally large drainage area achieved allows water to be circulated through the jar without outflow currents carrying organisms to the bottom. Jars stand in a continuously replenished water bath thus fluctuations in water temperature caused by ambient air temperature are very low. Pre-filtration of seawater was necessary in areas of high phytoplankton concentration because detritus clogged the 60–70 micron sized pores in the jar filters. Construction details of jars, prefilter and plumbing systems are described.

Introduction

Pelagic marine fish eggs are of the same density or lighter than seawater, and therefore their culture in running water presents difficulties not normally encountered in the culture of demersal eggs. Pelagic fish eggs usually hatch in an embryonic or prolarval condition (Hubbs, 1943) and newly born fish float with positive or neutral buoyancy while undergoing further development. The embryonic period, therefore, is composed of two phases, the free-floating egg stage, and the free-floating prolarval stage, when development of the eyes, digestive system, and mouth is completed.

In hatchery jars commonly used for incubating demersal fish eggs, the weight of the eggs and larvae is sufficient to overcome the lifting action of inflowing water; thus they are not lost over the top of the jar if water flow is adjusted properly. A similar system is unsatisfactory for pelagic fish eggs and prolarvae because the buoyant eggs are soon carried by currents to the outflow, where they are lost, or clog the exit if it is screened. Newly hatched prolarvae will free themselves when first carried by a steady current to an outflow screen, but are eventually killed by the repeated contact because they are unable to escape being trapped in the current.

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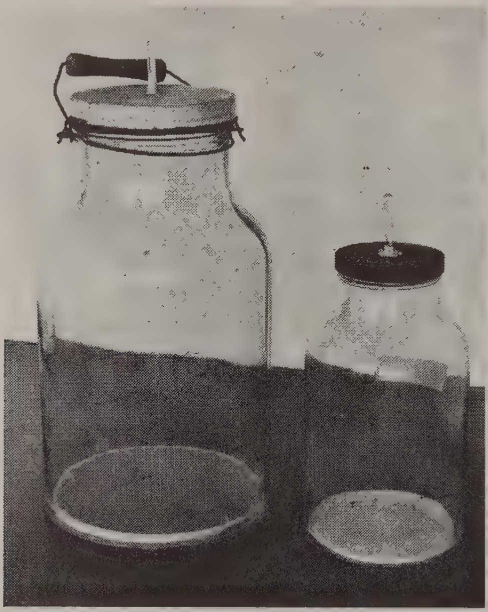

Figure 1. Culture jars with porous polyethylene bottoms. Large jars of 9 litre capacity (left) have bails to facilitate handling. The 7·5 cm diameter neck of the 2·5 litre jar (right) allows convenient handling of this jar, even when wet.

The use of bowls and jars to incubate pelagic fish eggs and to hold developing larvae (or other marine organisms) is often impractical, especially on shipboard during rough weather, and studies of development may be influenced by changes in pH, salinity, and oxygen and carbon dioxide content that may occur in static seawater. TEMPLEMAN (1948) noted that larvae of the lobster (*Homarus americanus*) reared experimentally in jars of static seawater had significantly reduced growth at moulting and extended intermoult stages compared to lobster larvae in nature. TÅNING (1952) reviewed changes in meristic characters of fish larvae related to differences in environmental conditions such as temperature, salinity, and oxygen and carbon dioxide tension. Many marine bacteria multiply rapidly in static seawater (WAKSMAN and CAREY, 1935; ZOBELL and ANDERSON, 1936), and may influence survival or development of fish eggs (SHELBOURNE, 1963; OPPENHEIMER, 1955), or oyster larvae (WALNE, 1958). Despite these disadvantages, bowls and jars have been the only generally available containers for holding marine organisms in the laboratory or on shipboard.

Construction Details of Culture Jars

To meet the needs of this laboratory's programme of rearing pelagic fish larvae, an easily managed and practical culture jar was developed to allow small marine organisms to be held in running water. This development was

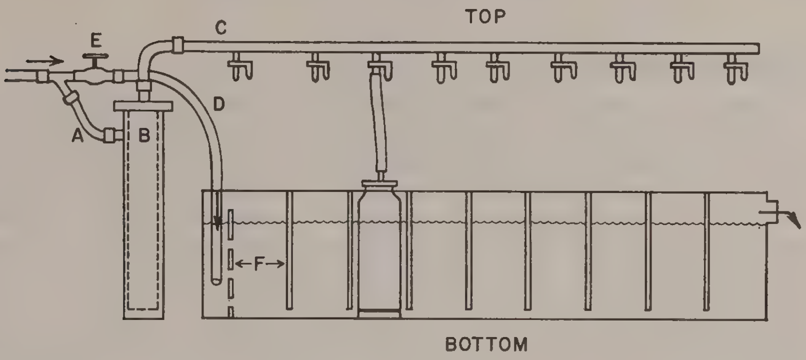

Figure 2. Shipboard installation of a battery of culture jars. Water from a main stream of seawater is divided into two branches. One enters the outer polyvinylchloride (PVC) casing of the filter cylinder (A) (see Figure 3 for the construction details) flows through a porous polyethylene filter (B), and enters a 2·5 cm diameter PVC pipe that has taps to individual culture jars (C); the second branch (D) by-passes the filter, irrigates the water bath holding the culture jars, and provides fresh water at sea temperature as needed when additional jars are put into use. A slight back pressure is created in the branch to the filter cylinder and jars by adjusting the hand valve (E) on the main line. Baffles in the trough (F) prevent water from surging back and forth when the ship rolls.

facilitated by the appearance on the market of a relatively inexpensive, rigid polyethylene filter material which can be easily worked and is obtainable in various thicknesses and pore sizes (Bel-Art Products, Pequannock, New Jersey, USA). The filter material used in the construction of the jars described here is about 3 mm thick and has a pore size of 60–70 microns.

The culture jars shown in Figure 1 have plastic screw caps containing water inlet tubes, and porous polyethylene bottoms. A hole was bored through the screw cap to receive a plexiglas tube, which was fixed in place with epoxy resin. A rubber gasket cemented to the underside of the cap provides an airtight seal when the cap is screwed to the jar. A small air space is left below the cap; the volume of flow can be judged from the size of the inflowing stream, and regulated. The glass bottoms of the jars were removed by cutting the jar walls, just above the curved basal portion, with a carborundum glass-cutting disc. In practice it was practical to rotate the jar against the cutting disc deepening the circumferential cut rather than attempting to cut through the jar from side to side.

The polyethylene filter discs were sealed to the jar walls with Dow-Corning RTV silicone rubber. This putty-like compound cures into a tough, clear, flexible rubber. Discs for jars were cut to size individually by standing a bottomless jar on a sheet of filter material, scribing around the inside with a sharp pencil, and cutting by band saw. The disc was forced up inside the jar for approximately one centimetre so that a bead of rubber applied around the wall under the disc would offer support as well as seal off spaces between the glass and the edge of the filter. The wide mouth of 9 l jars allowed the insertion of one's hand for application of a bead of rubber around the bottom to seal off spaces between the glass and disc; for small jars, a long applicator was used.

Results

Testing the apparatus at sea

A number of culture jars were tested during various cruises of the Bureau of Commercial Fisheries research vessel "Black Douglas". In southern areas a free-flowing stream was maintained in the ship's seawater system to avoid increases in water temperature. The jars required such a small volume of water (1 to 10 l per hour depending upon the number of jars used) that it was necessary that the distance be short between the main free-flowing water source and the culture jars, to reduce heat absorption in the water line. The most successful system employed is shown in Figure 2. The continuously flowing stream of water could be tapped at intervals to provide new fresh water to individual jars as required. The volume of flow to each jar was controlled by regulating the valve on the main line to create a slight back pressure through the filter to the dispensing pipe, and by adjusting the petcock on the pipe leading to the jar.

Jars of 2·5 l capacity were put in a trough, which acted as a water bath. This trough was continuously replenished by the waste water from the jars and from the main free-flowing stream. Fluctuations in water temperature in the jars were slight (less than 0·5°C), even when uncovered jars were exposed to strong sunlight and high temperatures on deck. In practice, however, the trough was covered by canvas when used on deck, to shield jars containing fish larvae or other organisms from strong light. Most organisms, particularly fish larvae, reacted to strong sunlight by congregating at the bottom of the jars. In subdued light fish larvae and copepods remained distributed throughout the jars and easily avoided contact with the bottom. When a flow of about 2·5 l per hour was maintained, strong swimmers, such as euphausiids, mysids and crab larvae swam freely over the approximately 120 cm^2 of filter in the 2·5 l jar, without being drawn to the bottom by outflowing water.

Filtration of water entering jars

It was necessary to filter inflowing seawater when concentrations of phytoplankton were high because algae and detritus clogged the bottoms of the jars and reduced the rate of water flow. Salps drawn into and ground up by the seawater pump caused particular difficulty because bits of jelly spread out and clogged large areas of the polyethylene bottoms. The filter illustrated in Figure 3 was designed for ease of cleaning and replacement of the filter cylinder. Organisms and debris larger than 40 microns are removed. A disposable outer sleeve of rice paper or coarse filter may be fitted over the filter tube to trap bits of medusae or salps, which tend to be drawn deeply into the polyethylene. Spraying the surface of the filter tube with a jet of water is usually sufficient to remove adhering particles, but the filter can also be cleaned in acid without damage. Two filter tubes were kept on hand, so that one could be cleaned while the other was in use. As shown in Figure 2, the filter cylinder received only the water passing to the dispensing pipe (not the entire flow of the main line).

Jars could be removed from the trough without loss of water by replacing the cap containing the water inlet tube with another cap. Since air does not

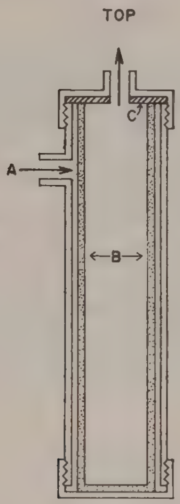

Figure 3. A primary filter to clean water entering culture jars. Water enters the outer casing (A) and percolates through an inner, porous, 40-micron polyethylene filter tube about 600 cm long (B). Filter tubes are exchanged by unscrewing the bottom cap on the cylinder. After insertion of a filter tube, the bottom cap is screwed tight; this seats the tube on a soft rubber gasket (C) in the upper cap.

enter the top of the jar when the cap is in place, water does not flow out through the dense bottom filter. The jar top may be removed and samples obtained without loss of water if the jar is placed in a larger glass container in which the water rises to the same level as in the culture jar. Because the investigator can see through the walls of the glass container, the capture of particular specimens by pipette is facilitated. This is an important consideration when delicate invertebrates or fish larvae must be captured repeatedly for examination or measurement.

Summary

1. The replacement of glass bottoms of jars with porous polyethylene filters permitted the circulation of seawater through the jars.

2. Continuous flushing of jars avoided increases in metabolite level and bacteria.

3. Buoyant pelagic eggs and early stage larvae are not drawn to the bottom filter because the large area of outflow reduces water velocity.

4. Instructions are given for the construction of jars and a shipboard culture-jar battery.

5. In areas of abundant phytoplankton a filter (construction details given) was used to remove debris from water entering jars.

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(O16) ● Gunter R. Seckel (Bureau of Commercial Fisheries Biological Lab., Honolulu, Hawaii), *The Trade Wind Zone Oceanography Pilot Study.* As a part of a pilot study for a more extensive investigation in the trade wind zone of the North Pacific, the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, completed an 18 months' observational program near Hawaii in July 1965. A grid of oceanographic stations in the area bounded by lat. 10°N, 26°N, and long. 148°W, and 157°W was occupied at monthly intervals. The aim of the Trade Wind Zone Oceanography pilot study is to develop a model that explains changes in the distribution of temperature and salinity in terms of seasonal changes in the net heat and water exchange across the sea surface, wind stress, and the effects of water motion. Preliminary results indicate that the approach is feasible. Within the upper 300 m of the study area, water masses are found that extend from lat. 40°N to 35°S at the sea surface. Subsurface temperature and salinity fronts associated with boundaries of the major water masses are of the same order of magnitude as those at the sea surface. Subsurface frontal movements or displacements are of the same order of magnitude as those at the sea surface. Geostrophic computations show that the generally westward flowing North Equatorial Current contains large eddies and eastward-flowing components. Relatively high current speeds are associated with water mass fronts. A multiple ship operation in the area 0° to lat. 30°N, long. 130°W to 180° lasting 18 months to 2 years is planned.

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Geophysical Union, vol. 47, no. 1,
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OCEAN ENVIRONMENT AND FISH DISTRIBUTION AND ABUNDANCE

Oscar E. Sette
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Abstract

For U. S. fisheries to grow, they must become more efficient than those of other countries, as have most other industries, in order to overcome the high wage-price structure associated with our high standard of living. A major obstacle to efficient, systems-integrated fishery operations is the wide fluctuation in the abundance and distribution of fish, especially the pelagic schooling species which have the highest potential for providing increased catches. It is proposed that fish hunting time be reduced and flow of fish to port be smoothed by forecasting the time and place that concentrations of catchable fish will occur.

This requires (1) research to establish the environmental conditions conducive to fish concentrations, (2) research to determine the reaction of the ocean to the variations in the overlying atmosphere. For both (1) and (2) information is needed on ocean conditions, with time and space continuity, ocean-wide and down through the upper layer and well into the permanent thermocline. To provide this information an extensive ocean monitoring system is proposed to serve, along with the established weather monitoring system, the needs held in common by the military, the fisheries, the meteorologists, the physical oceanographers, the biological oceanographers, the radiologists and the pollution-control specialists.

INTRODUCTION

One of the marvels of these times is that the United States, with its high standard of living, has managed to keep its products competitive in the world market. One of the striking exceptions to this generality is the fishing industry. Ten years ago, 70 percent of the U. S. fishery supply came from domestic fish catch. In 1964 this had fallen to 38 percent. It probably is still lower now. We are a net importer of fishery products by a substantial margin.

There are a number of reasons for this. One of them, and I believe it to be a major one, is that the fishing industry, unlike most other American industries, does not lend itself to the American genius for applying technology and systems research and management, which produces goods at prices competitive with those of the rest of the world despite our higher costs of materials and manpower.

A large obstruction, if not the major one, to attainment of the modern systems type of operation at the fishing level is the variation in abundance, location and catchability of the fish. Too large a portion of time is spent hunting for fish, too little for catching them. On occasions when the fleet comes upon good fishing, its landings glut the market and there is either a price reaction or, sometimes, a failure of the market to handle the fish. Often the net effect on the fisherman is an income less

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than his needs for keeping his vessel and gear in repair and replaced when worn out, and less than is needed to keep him and his sons in the fishery, while the higher income and greater security of shoreside employment offer a better life. The effect on the processor or the wholesaler is a highly irregular supply of domestically caught fish. Since frozen fish have become a common international commodity, he can offset these irregularities by imports. No doubt this, as well as price advantage, has been a powerful factor in making this country a large net importer of fishery products.

If this crude and overgeneralized statement is essentially correct, and if we wish to avoid slipping into further dependence on imports for our supply of fishery products, then it is logical to look into the causes of the irregularities in fish catch. If we can identify them and adopt measures to avoid them, or even make use of them, we will have a powerful tool for increasing the efficiency of fishing, processing and distributing our domestic catch. If we can fashion this tool and employ it successfully, we should greatly enhance the capability of our fisheries to compete with those of the rest of the world.

FISHERY FLUCTUATIONS

My thesis is that changes in the ocean environment cause major changes in fish distribution and abundance and thereby produce irregularities in fish catch. There are substantial differences in the amplitude of fluctuations in the catch of the various kinds of fish. In general the catch of bottom fishes like the cod, haddock, flounder, sole, halibut, etc., fluctuates less than the catch of most other types of fish. In contrast, the pelagic, near-surface swimming and schooling fishes fluctuate the most widely in abundance and especially in distribution. Among these are the tunas and tuna-like fishes, the mackerels and the herrings and many another. This type of fish never remains in the same ocean area in fishable concentrations for any length of time within the season or from year to year. It is this group of elusive fishes that affords the largest potential for production.

A few examples drawn from the historical record illustrate the year-to-year variation in catch of several kinds of these pelagic schooling fishes. Years of painstaking study have identified two general causes of variation in catch, quite apart from the variations in amount of fishing effort expended.

One of these is the variation in the over-all abundance of a species caused by year-to-year variation in the infant mortality. Seemingly regardless of the amount of spawning, some years many young survive through the larval and juvenile stages and grow to commercial size, and in other years very few survive. Figure 1, of the western Atlantic mackerel catch, shows variations which may be predominantly caused by such variations in infant survival.

During the 19th century the mackerel was one of the mainstays of the New England fishery, and a major food item. There was a barrel of salt mackerel along with the cracker barrel in almost every grocery and general store. Then in two years (1885-1886) there was a catastrophic decline in catch of about 90 percent. Great distress was caused in the fishing ports, and salt mackerel became a minor food commodity. It remained so for 40 years. Then there was an upsurge in the middle 1920's. At that time I was studying the biology of the mackerel. In 1926 I found that the catch was composed almost entirely of two ages: 3-year-olds and 5-year-olds. The latter of course were spawned in 1921 and the former in 1923, and may be called the 1921 and 1923-class, respectively. In subsequent years I found the 1928, 1931 and 1933 classes to have been outstanding, whereas the survival from intervening spawnings was trivial. From the 10-year sample of age compositions in the catch, it was obvious that the infant mortality was nearly total in over half of the years. It appears probable, though we never can be sure, that variations in infant mortality were responsible for most of the year-to-year fluctuations in catch.

The other type of fluctuation is caused by variations in distribution. This changes the proportion of the fish population that comes within the range of the fishery. Fig. 2, of the catch of albacore tuna along the Pacific coast of the United States, most probably exemplifies variation in distribution rather than variation in over-all abundance. We did not know it at the time, but it has since been proved by mid-ocean fishing and by tagging that the albacore is distributed from one side of the Pacific to the other, and our coastal fishery catches them only in summer when warm water conditions usually prevail and the albacore approach near enough to the coast for the small boats to reach them. We now feel quite sure that what seemed to be nearly total disappearance between 1926 and 1938 was merely the failure of albacore to come far enough toward the coast for our fleet to reach them. The generally higher level of catch after 1940 than before 1926 probably is due to a combination of (1) an increased use of temperature information by the albacore fishermen, (2) a modest increase in the range of their boats, and (3) a spread of the fishing from southern California northward along the Oregon and Washington coasts.

Bluefin tuna, Fig. 3, is probably another example of this kind, though we know less about the migrations of this species. Like the albacore, this tuna appears along the American coast briefly during summer and fall. Most of the catch is taken off Lower California. The irregularities probably depend on how large a portion of the bluefin population approaches the coast and how close it comes. In any event, the catch fluctuates irregularly from less than one thousand tons to over ten thousand tons.

CHANGING OCEAN CONDITIONS

Most oceanographic information is confined to the average or supposedly typical ocean. We are now beginning to learn about changes in ocean conditions. In our laboratory at Stanford University, we /J. F. T. (Ted) Saur, L. E. (Larry) Eber and I/ analyzed the sea surface temperatures for 1956 and 1957 as collected by the Marine Weather arm of the Weather Bureau and archived at the National Weather Records Center, Asheville, N. C., for each month of 1956 and 1957. Figures 4 and 5, taken from U. S. Bureau of Commercial Fisheries Circular No. 134, give the analysis for June of each of these years. The difference between these Junes is given in Fig. 6. Most of the eastern Pacific and Tropical area was warmer in 1957 by varying amounts up to 4°C. (or 7°F.), whereas much of the western Pacific, and a tongue extending eastward in mid-latitudes, was colder by a similar amount. From perusal of the charts for the other months of the year, it appears that this general feature of warmer water in the eastern Pacific and colder in the western Pacific developed early in the year and persisted through the rest of the year, though with many striking differences in detail.

To us, as warm-blooded animals, having a physiologically controlled internal temperature and further protected by clothing and shelter against a far wider daily and annual atmospheric temperature range, a change of 7 degrees may seem trivial. But to cold-blooded animals that live in the sea, this would be a very large change indeed. It has been aptly stated that cold-blooded aquatic animals are slaves to their environment. A variation of a very few degrees in temperature greatly affects their rate of metabolism, the amount of their activity, and the amount of food needed to sustain their activity. It is not very surprising that they have evolved habits, reactions, and migratory patterns which, in some species at least, tend to keep them in a relatively narrow range of temperature which, to each species, is nearly optimal. Each such species changes its location so as to stay within its optimal temperature range.

One such change, as from 1956 to 1957, and observed mainly in only one ocean condition, surface temperature, is not sufficient for drawing any conclusions between ocean conditions and infant mortality or between ocean conditions and the distribution of commercial-sized fish, although we know that in 1957 the distribution of a number of kinds of fish was quite different than in the immediately preceding years. Fish distribution can vary in three dimensions and fish certainly are sensitive to a number of conditions in addition to temperature. What is required at this stage of our ignorance are means for measuring the appropriate conditions in the three dimensions and their change with the fourth dimension, time, until we find out through a combination of at-sea observations and controlled experiments in the laboratory what the appropriate conditions are. Both the identification of appropriate conditions, and their measurement in the sea, are formidable and complex problems. I shall deal further, only with the problem of measuring ocean conditions as the one of most immediate interest to members of the Marine Technology Society and of most general concern to many other segments of the scientific, technological, and ocean engineering community.

What is needed, in my personal opinion, is information, with space and time continuity, on ocean conditions, such as temperature, salinity and probably other conditions of significance to biological activity, such as oxygen concentration, water clarity, etc., not only at the surface but also down through the mixed layer and well into the permanent thermocline. This means down to a depth of 600 meters (2000 feet) in much of the ocean and to 1000 meters (3300 feet) in a number of areas.

AN OCEAN MONITORING SYSTEM

Such data are also needed for other purposes. Through multiple contacts, I have become aware that the paucity of data also faces a number of ocean-oriented groups. To enumerate those groups that come readily to mind--(1) the meteorologists concerned with air-sea interactions, (2) the physical oceanographers concerned with processes causing variations in the sea, (3) the biological oceanographers interested in dynamic ecology of communities of ocean organisms, (4) the fishery-oceanographers concerned with the dynamic ecology of seafood organisms, (5) the radiologists concerned with the diffusion of radionucleides in the sea, (6) the military scientists concerned with the acoustic channels in the ocean, and (7) the pollution scientists concerned with the near-shore and oceanic dispersion of pollutants.

All of these, I believe, have a common need for certain ocean information with some degree of continuity in time and space, though with some variation in the required degree of resolution in time and space and perhaps considerable variation in the required properties to be measured. This suggests a basic atmosphere-ocean monitoring system to serve as many of the needs held in common among the users as are practicable to serve in terms of the state of technology and of the procurable funding.

This leads me to envision a basic network consisting of:
1. The ships of opportunity presently cooperating in sending to the Weather Bureau 6-hourly marine weather reports, and provided with improved instrumentation for measuring near-surface sea temperatures;
2. Selected ships of opportunity equipped with expendable bathytermograph (XBT) systems to probe the sub-surface ocean, analogous to the already established radiosonde system for probing the upper atmosphere;
3. Automatic deep-anchored buoys, located in areas not traversed by steamer lanes, for measuring the customary atmospheric conditions plus a string of sensors measuring water properties at a number of levels down to at least 600 meters and deeper in some areas;
4. Existing tide stations, plus additional ones strategically located with reference to major ocean currents, and with certain of the tide gauge stations supplemented with weekly sub-surface observations in the adjacent ocean as was provided at many stations during IGY;
5. Airplane over-flights with infra red temperature sensors, and perhaps XBT capability, covering critical areas not otherwise monitored; and
6. Cloud cover charts assembled from satellite photographs.

For efficient deployment of these facilities, and for maximal return of information from the data they produce:
1. The design of such a network should be jointly determined by both the research users and the operator users;
2. The processing and communication of the information should be adaptable to users' needs; and
3. Quality control should be insured by the current study of the data--this being, in our experience, the most reliable insurance.

ANTICIPATED BENEFITS

With such a system in being, the way will be cleared for developing prediction capability. Of course, the information from the system alone will not be sufficient. In general, prediction of ocean conditions requires that the variable kinetic and thermal energy exchanges between the atmosphere and ocean be better measured and become more thoroughly understood, especially as to phase lags. For fishery prediction, the behavior of fishes toward environmental change must become better understood and quantified through laboratory experiments and through observations at sea. It can be expected that the atmosphere and ocean monitoring will serve to greatly accelerate the progress toward sufficient understanding of atmosphere-ocean relationships and fish and ocean environmental relationships.

It is to be expected also that the larger scale and larger amplitude changes in ocean conditions will be more readily predicted than the smaller and more transient effects. Similarly the larger and more extensive changes in fish abundance and distribution will be more readily observed and predicted than the very local and less pronounced changes. It may be envisioned that the eventual fishery forecasting system would consist of periodical medium and long-range general predictions of probable unseasonable abundances and locations of fish concentrations to guide the forward planning of fishermen and processors. Added to these would be more frequent, perhaps daily, advisories of current conditions on a real-time basis radioed to fishing vessels at sea to indicate which direction to sail with the best probability of encountering catchable concentrations of fish. Fishermen themselves may have advanced instrumentation aboard ship by which to further guide the deployment of their gear.

With these aids, together with technological improvement of fish catching devices, the era of week-long, month-long and year-long spells when the fleet cannot find the fish schools, or when they can find only a scattered few, should end. The flow of fish into landing ports should become steadier and the American genius for organizing efficient production systems will be able to play as large a part in keeping the domestic fishery competitive with the rest of the world, as it does now in many other industries.

That this is not an idle dream is proved by the experiences of the Bureau of Commercial Fisheries Tuna Resources Laboratory at La Jolla, California, in predicting, from April sea surface temperatures, when, where, and in what quantities the albacore will appear along our Pacific coast in summer. After several seasons of fair success, last summer the prediction went awry owing to a reversal between April and June in the seasonal warming trend, which retarded and diminished the early summer run. However, during the same summer the Laboratory also experimented with nearly daily radio advisories to the fleet. In one instance at least, and there may have been others, there was issued an advisory of suitable temperature conditions far north of the then area of fleet fishing. As a result, the fleet was led to an area of excellent fishing, days ahead of their normal occupation of this area. As a result, a significant tonnage was added to the season's catch. (Glenn Flittner, personal communication.)

Finally, it should be noted that the basic observation network and the attendant research here suggested as a tool for increasing the efficiency of fishing operations could also increase man's ability to select conservation measures appropriate for the wise use of fishery resources. Wide fluctuations in apparent abundance of fish can obscure trends imposed by overfishing; also, declines in catch from natural environmental causes, especially if prolonged, can be mistaken as evidence of overfishing. With the successful operation of the observation network, together with achievement of an understanding of the quantitative effects of environmental changes, it will become increasingly possible to "screen" out the noise of environmentally induced fluctuation and leave revealed the more fundamental trends related to the effect of fishing.

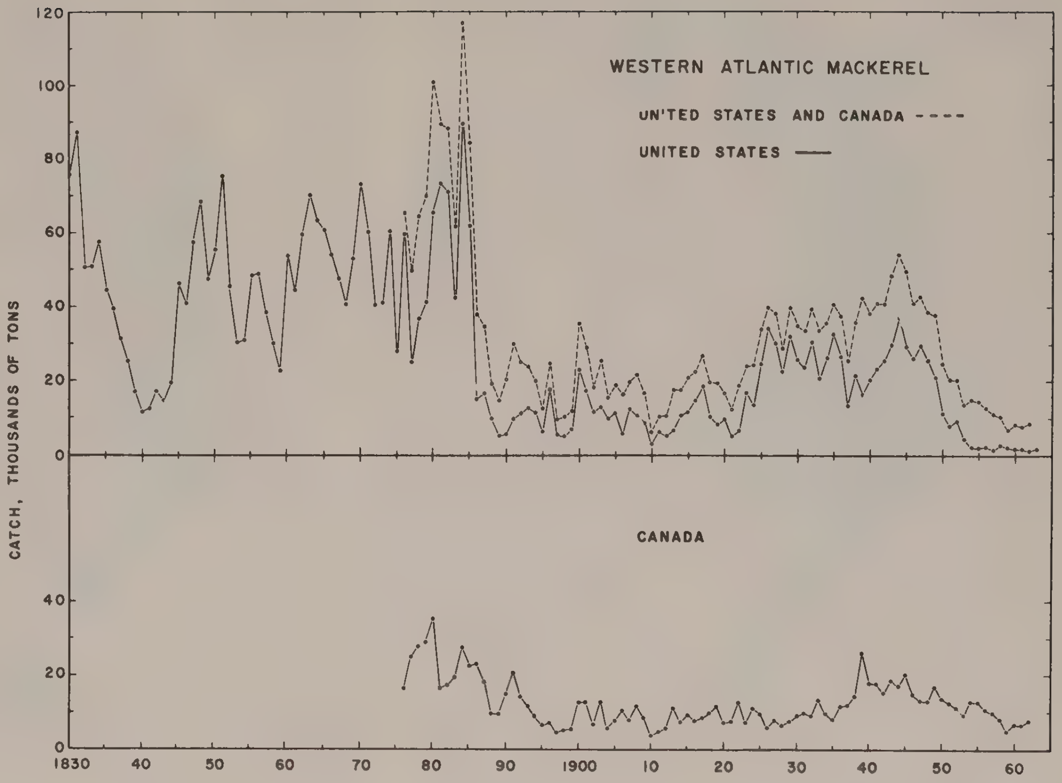

Fig. 1. Catch of mackerel along the Atlantic coast of the United States. Source: U. S. Bureau of Commercial Fisheries statistical reports.

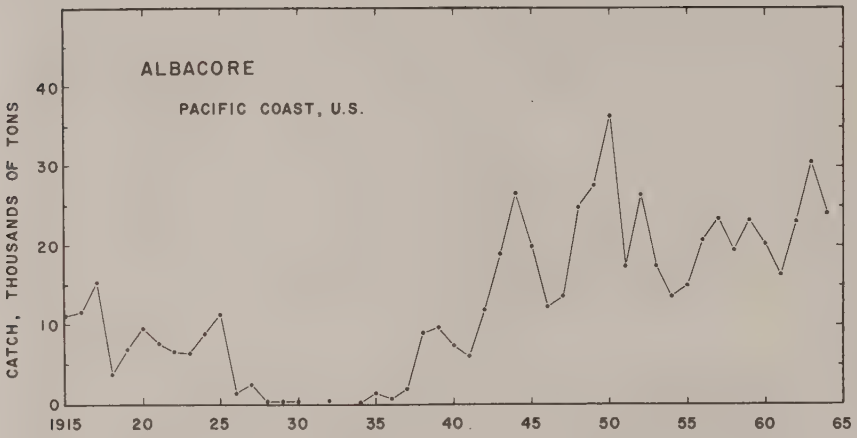

Fig. 2. Catch of albacore tuna off the west coast of the United States. Source: U. S. Bureau of Commercial Fisheries statistical reports.

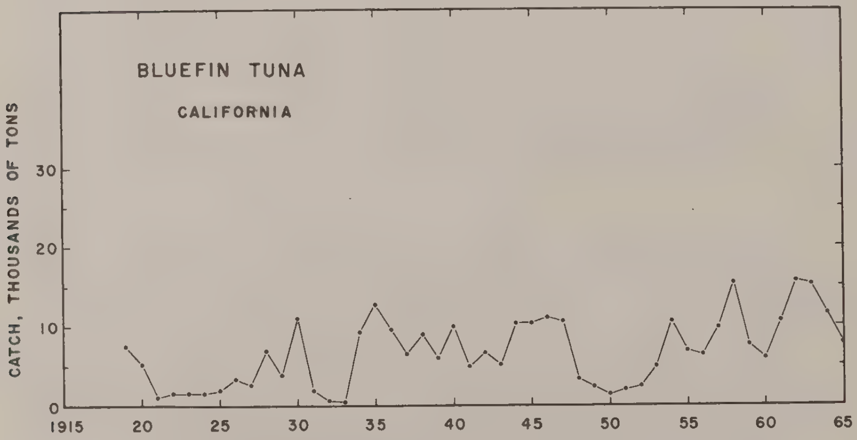

Fig. 3. Landings in California of bluefin tuna from waters off the west coast of North America. Source: U. S. Bureau of Commercial Fisheries statistical reports.

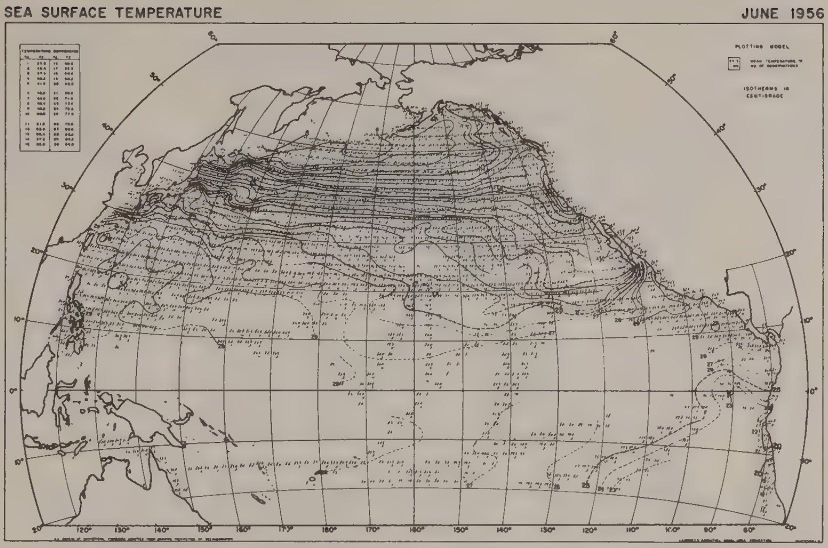
SEA SURFACE TEMPERATURE
JUNE 1956

Fig. 4. Mean sea surface temperature (°C.) of the Pacific Ocean in June 1956. Reproduced with severe reduction from U. S. Bureau of Commercial Fisheries, Circular 134.

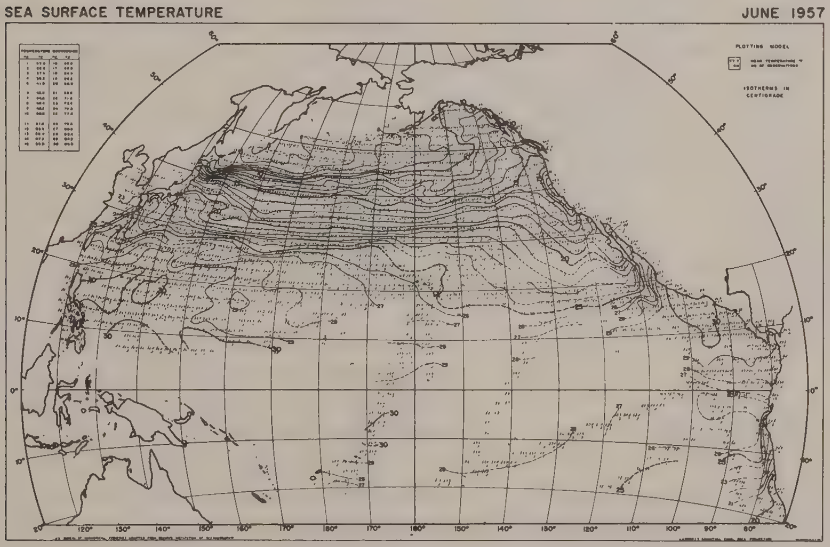
SEA SURFACE TEMPERATURE
JUNE 1957

Fig. 5. Mean sea surface temperature (°C.) of the Pacific Ocean in June 1957. Reproduced with severe reduction from U. S. Bureau of Commercial Fisheries, Circular 134.

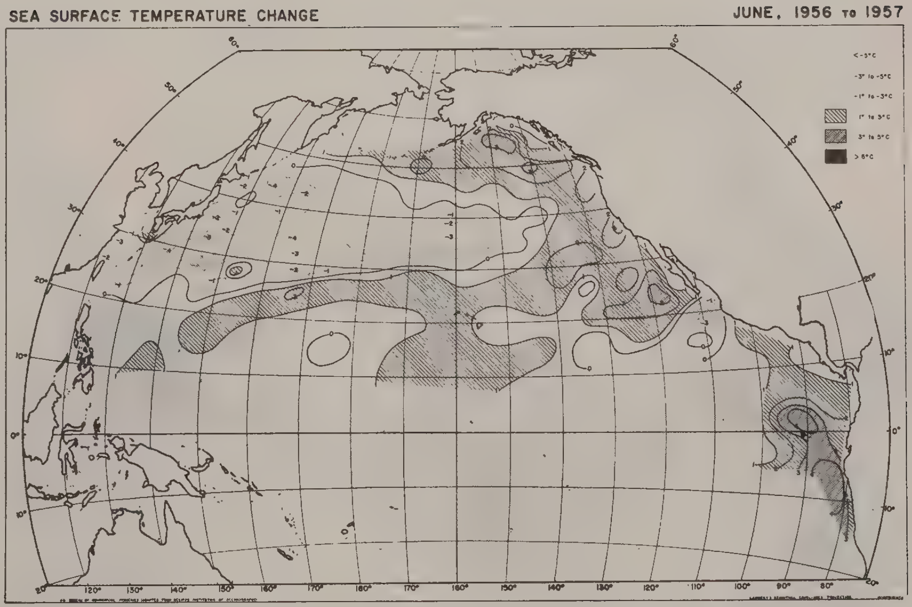
SEA SURFACE TEMPERATURE CHANGE
JUNE, 1956 TO 1957
< -5° C
-3° to -5° C
-1° to -3° C
1° to 3° C
3° to 5° C
> 6° C
120°
130°
140°
150°
160°
170°
180°
170°
160°
150°
140°
130°
120°
110°
100°
90°
80°
60°
50°
40°
30°
20°
10°
0°
10°
20°

Fig. 6. Sea surface temperature difference (^{0}C.) between June 1956 and June 1957. Negative values indicate areas colder in 1957 than in 1956.

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REPORT OF THE WORKING GROUP ON SKIPJACK TUNA

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Chairman

and

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Bureau of Commercial Fisheries Biological Laboratory
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GEOGRAPHIC DISTRIBUTION

The horizontal distribution of the skipjack tuna in the North and South Pacific is bounded by the approximate position of the 20° C. (68° F.) surface isotherms (fig. 1). This region extends poleward from the Equator to about the 40th parallel of latitude in the Northern Hemisphere and to about the 35th parallel of latitude in the Southern Hemisphere--a sea area of about 30 million square nautical miles.

These limits are based on three lines of evidence: (1) the distribution of present and past skipjack tuna fisheries, (2) the distribution of larvae, and (3) the distribution of sightings and occasional captures. The distributional evidence was treated in detail in an earlier publication (Bureau of Commercial Fisheries, 1963). We do not imply, however, a cause-and-effect relation between the 20° C. isotherm and the distribution of the fish; we merely use this particular isotherm as an index of location. Skipjack tuna have not been taken from some regions within these isothermal boundaries, but this may easily be owing to inadequate exploration. It should be recognized that the isotherms given in figure 1 are in their average position and that they may be displaced in any single year or month. These displacements, however, would represent only a small portion of the total range of the fish. Only two large fisheries lie within this great area--one along the North, Central, and South Americas, and the other along Japan and the island chains extending southward. The recent annual production of these fisheries was 68,000 and 167,000 metric tons, respectively. In addition, a small midocean fishery in Hawaii produced 5,000 tons. New fisheries have begun in Australia and the Palaus, but these have not yet been firmly established.

VERTICAL DISTRIBUTION

On the basis of vertical distribution of temperature and of larvae we infer skipjack tuna probably range from the surface down through the warm upper mixed layer and possibly down into the upper portion of the thermocline. Both temperature and dissolved oxygen are likely to have an important influence on

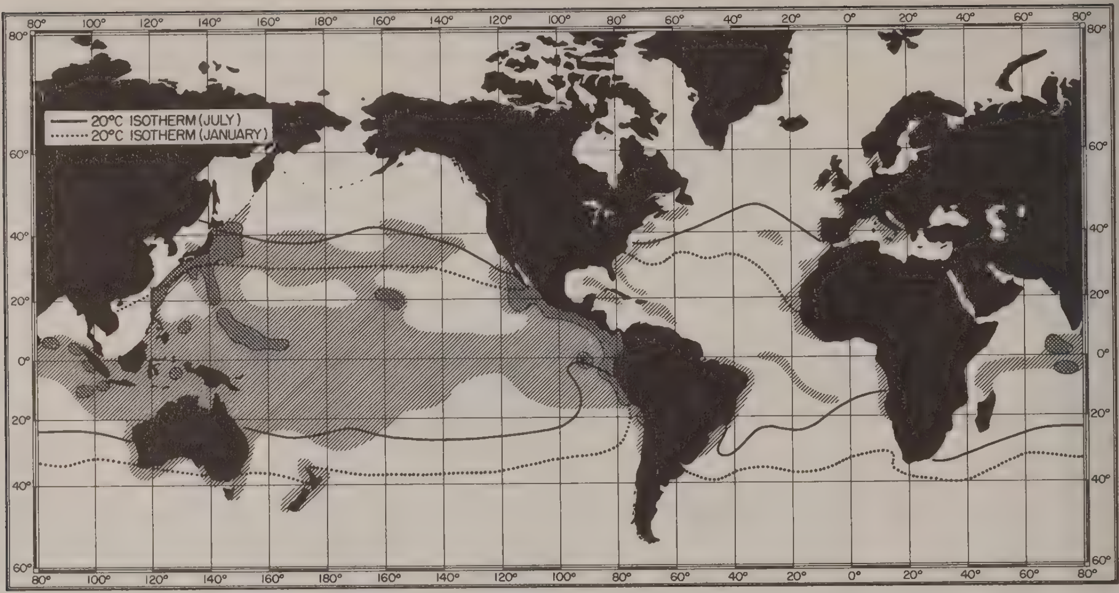

Figure 1.--World distribution of skipjack and skipjack fisheries (from Bureau of Commercial Fisheries, 1963).

the maximum depth at which skipjack tuna normally swim.

Interesting observations pertinent to the vertical distribution of skipjack tuna were made in late 1965 off the coast of Oahu from the research submarine Asherah. The fish were observed at depths of 250 to 550 feet (Strasburg et al. MS.[1]). Although no temperatures were recorded simultaneously with the observations of the tuna, temperature observations during the cruise at a depth of 125 m. (500 feet) ranged between 18° and 20° C. (about 6° C. less than the surface temperature). This suggests that skipjack tuna might penetrate into the thermocline. These observations were along the precipitous subsurface portion of Oahu, however, where turbulence can be expected to cause temperature gradients which might not be typical of those in the open ocean.

SUBPOPULATIONS

''Subpopulation'' is used here in the sense of a portion of a population which is independently self reproducing; that is, it does not interbreed with other portions of the population. The evidence for existence of subpopulations of skipjack tuna is of two types. One, mainly inferential, is discussed in the next section of this report on hypotheses; the other, from immunogenetic data, is based on comparisons of the relative frequency of different blood types in samples from the population.

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[1] Strasburg, D. W., E. C. Jones, and R. T. B. Iversen. MS. Use of a small submarine for biological and oceanographic research. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii.

Initially, differences were recognized between samples taken from several central Pacific regions. Frequencies of antigens were distinctly different between samples taken in the waters adjacent to the Marquesas, Tuamotu, and Society Islands, and these samples were very dissimilar to samples from Hawaiian waters. Somewhat later, clear evidence was obtained that at least two subpopulations of skipjack tuna enter the Hawaiian fishery. A single large sample from the Western Caroline Islands was also found to be sharply different from all other samples tested.

One of the reagents used in these early studies is no longer available, but several additional, better reagents have been developed.

Generally, it appears clear on the basis of differences in antigen frequencies, which were much greater between than within subpopulations of the North and South Pacific, that marked subpopulation divergence has occurred between these two areas and to a lesser, but recognizable, extent within them.

At present work is in progress along two lines of inquiry to obtain genetic information for subpopulation identification. Blood group antigen studies and electrophoretic studies of inherited protein variation in the serum are now being supported by the Bureau of Commercial Fisheries Biological Laboratory, Honolulu. Electrophoretic studies of various proteins are being made by the Inter-American Tropical Tuna Commission.

Although immunogenetic techniques have not yet been applied adequately to investigate the subpopulational relation between the skipjack tuna of the eastern Pacific fishery and those west of this fishery, a number of other items of evidence may be pertinent to this subject. Taken in combination they strongly suggest that successive cohorts of skipjack tuna enter the area of the eastern Pacific fishery, remain available to the fishery for only a few months and then depart, probably to the westward at least as far as the central Pacific Ocean. These are:

1) The effect of the California fleet's fishery on the abundance of this stock is so slight as to be undetectable by conventional population-dynamics analysis.

2) The fishery in the eastern Pacific takes very few fish old enough to be even approaching maturity.

3) Plankton tows in the eastern Pacific take few larvae (see fig. 2) in relation to the numbers of fish of commercial size caught there.

4) Skipjack tuna larvae are taken much more commonly in plankton tows in tropical and subtropical waters to the westward in the broad band across the central Pacific.

5) Three skipjack tuna, small when tagged in the eastern fishery, were recaptured in the central Pacific--two in Hawaii after 21 and 28 months, respectively, and one in the Line Islands area after 16 months. All were much larger than when tagged. Of interest in this context is an immunogenetic determination that skipjack tuna in a small sample from the eastern Pacific fishery were indistinguishable from one of the two subpopulations in the Hawaiian fishery, identified with the same reagents.

6) Skipjack tuna much larger than those commonly caught in the eastern Pacific furnish the bulk of the summer catch in Hawaii, where they are called ''season fish.''

7) Large skipjack tuna are frequently taken incidentally on longlines in a

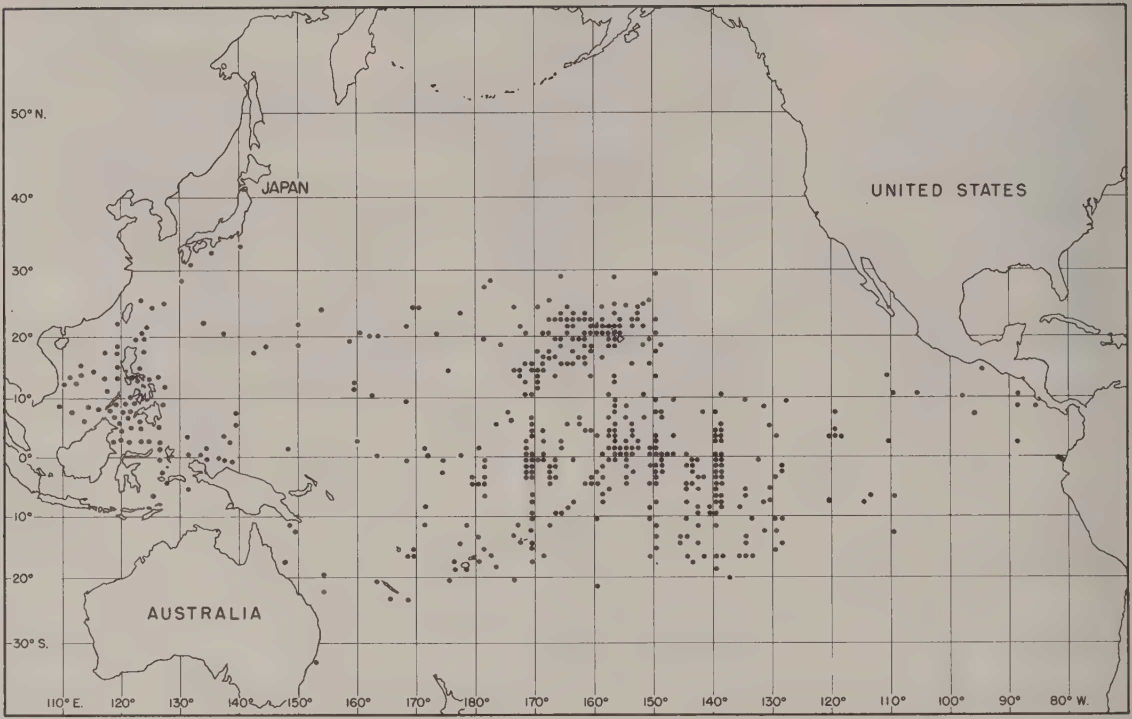

Figure 2.--Locations of capture of skipjack larvae 1949-65 (from Matsumoto, 1966).

broad band across the tropical and subtropical Pacific.

These items taken together are strongly suggestive, but not conclusive, evidence that considerable numbers of the skipjack tuna supporting the eastern Pacific fishery are members of a subpopulation that ranges far from the fishing area in later life.

HYPOTHESES

Two hypotheses concerning the relationships of the stocks among the several discrete skipjack tuna fisheries of the Pacific have recently appeared in publication.

The model given by Rothschild (1965) embraces several sub-hypotheses, but its central feature rests on the supposition, consistent with available evidence, that the skipjack tuna of the eastern and central Pacific spawn mainly in the central Pacific. The resulting young appear in the coastal and near-coastal fishery of the eastern margin of the tropical and subtropical Pacific, remain there only briefly during their ''adolescence,'' and then migrate to the central tropical Pacific, where presumably they feed and spawn during the remaining years of their lives.

This hypothesis of course implies a subpopulation extending at least from mainland America to midocean. It does not preclude the existence of other subpopulations. In fact Rothschild expresses doubt that the skipjack tuna in Marquesas-Society-Tuamotu waters conform to the pattern just sketched, thus implying one or more subpopulations with distinctive life regimes. An independent population (or complex of populations) in the western half of the Pacific is also implied.

The model of Kawasaki (1964) is similar in having the skipjack tuna along both the eastern and western margins of the Pacific (and of Hawaii) recruited from central tropical waters. He seems to imply a single interbreeding stock for the whole Pacific.

ESTIMATES OF BIOMASS AND YIELD

So little is known about the numbers and sizes of skipjack tuna stocks throughout the 30 million square miles over which they are distributed that no specific estimate of the total potential yield would have a factual basis. The potential catch must be very large, however, compared with the catches now being made in the relatively small portions of the tropical Pacific where commercial fisheries have become established.

For the stock or stocks of coastal North, Central, and South America, the data from the present fishery afford a slender basis for estimating the quantity which this population might yield if fished with appropriate intensity throughout the life of the fish instead of during only a brief period of their youth.

Two such estimates of potential yield were made (Silliman, 1966, and Rothschild, 1966). These estimates are based on roughly calculated or conjectured values for mortality, growth, recruitment, and period of exposure to the eastern Pacific fishery. Both estimates assume that the eastern Pacific fisheries harvest only relatively small skipjack tuna and then use this assumption to compute potential harvests for a full range of sizes. By implication (see preceding section on hypotheses), the larger fish potentially could be harvested in the central Pacific, or at least some significant distance west of the area of the present eastern Pacific fishery.

Silliman, assuming a 2-year exposure to the eastern Pacific fishery and an instantaneous mortality of 0.8, estimated a potential yield of 225,000 metric tons. This point estimate was derived from a simulation technique which reproduced the 1944-61 trend of skipjack tuna yield from the eastern Pacific reasonably well. But it is not a unique solution of the estimation problem. Other combinations of values assigned to coefficients and variables might match the trend equally well yet produce different estimates of potential yield. Rothschild, using a range of values for period of exposure to the eastern Pacific fishery (2 to 6 months), and of instantaneous total mortality (1.0 to 2.0), and employing the yield function tabulated by Beverton and Holt (1964), estimated potential yields ranging from 140,000 to 1,200,000 metric tons.

Despite the employment of different assumptions and methods, both authors arrived at potential yield estimates several times greater than the average annual catch of 68,000 metric tons taken from the stock or stocks of skipjack tuna fished in the eastern Pacific Ocean in recent years. The wide spread between the upper and lower estimates emphasizes the uncertainty attached to such estimates. One can only conclude that this stock or stocks could support a yield very much larger than the present one. In addition, there are the potential yields which might be afforded by still other stocks of skipjack tuna probably existing in an unfished state in the vast reaches of the tropical and subtropical Pacific Ocean, but for which there presently exists no basis for estimating potential yield.

IMPROVEMENT OF YIELD ESTIMATES

Great uncertainty attaches to the yield estimates just given. Estimates for a given subpopulation can be improved when a fishery is imposed on the whole subpopulation through its full range of commercial sizes and the intensity of fishing changes sufficiently to produce a measurable change in fishing mortality. This of course requires that adequate data on the fishery be collected, preferably from the inception of the fishery.

Of primary importance is the collection of statistics on catch, effort, and size distribution. Two aspects of basic data collection need emphasis. First, newly developing fisheries, such as that in the Palau Islands, require a careful documentation of statistics on catch, effort, and size distribution. Second, statistical documentation programs already in use need continued evaluation to ensure operational and statistical efficiency. In addition, sampling and analytical studies conducted on species of tuna whose fisheries use bait fishes may need to consider research designs in the context of two fisheries--a fishery for bait and a fishery for tuna superimposed upon that for bait.

In order to make useful estimates of the parameters that quantify measurements of population size, an understanding of subpopulation structure is necessary, because it is likely that each subpopulation has rates of growth, recruitment, and mortality differing from those of other subpopulations, and it is almost certain that each will be fished at a different degree of intensity. In particular the horizontal distribution of subpopulations of skipjack tuna needs to be elucidated. The studies which need to be conducted (by immunogenetic and serological techniques already developed) are investigations of the horizontal subpopulation structure between the eastern Pacific fishery areas and the central Pacific (from the latitude of Hawaii to the latitude of the Tuamotu archipelago); between the central Pacific and the western Pacific (in particular, between the fish taken in the Japanese fishery and those that occur among the islands to the south of the Japanese archipelago); and finally the inter- and intra-archipelago subpopulation affinities.

Completion of most of the immunogenetic and serological studies should enable the design of tagging experiments to elucidate further the movements of the various subpopulations and thus ascertain their contributions to the fisheries. The design of the tagging experiments must, of course, also consider the use of the accrued tagging data to estimate mortality and growth rates. Once the subpopulations can be identified in time and space, estimates of population parameters can be improved. Among them are rate of growth, recruitment, immigration, emigration, and mortality.

Studies of subpopulation structure and the causes for fluctuation in population size and catch require quantitative information on distribution of larval and juvenile skipjack tuna.

Finally, independent checks on yield estimates are needed. These might be pursued through studies of primary productivity and analyses of trophic level. These studies would provide not only crude checks on potential yield estimates, but much information on the transformation of energy throughout the biota. But the most decisive check is the measurement of results when a fishery is imposed on the stock in question; or in an existing fishery, when the nature and intensity of fishing are changed.

INFORMATION AND RESEARCH NEEDED

Some increase in yield of skipjack tuna in the already established fisheries can and probably will be generated by the fishing industry itself, especially if, as now seems probable, the demand for tuna increasingly leads the supply and, through effects on prices, adequately rewards the intensification of effort. For instance, in the fishery by the California tuna fleet, the catches of yellowfin and skipjack tuna have been correlated inversely during the last 16 years. Doubtless this is because yellowfin tuna command a higher price and therefore more effort of the fleet is directed toward catching them when they are relatively "catchable." But when natural fluctuations of yellowfin tuna make them less catchable, a greater proportion of effort is directed toward skipjack tuna. In the future, as yellowfin tuna become generally less "available," whether through overfishing or through regulation adopted to prevent or correct overfishing, more effort will be directed toward skipjack tuna. In addition the ingenuity of fishermen, coupled with general advances in technology, can be expected to make their effort more effective in the future, as happened in the past when the power block and nylon seine were adopted. In short, some increase in yield of skipjack tuna will result from an increase in fishing effort.

Similarly in Hawaii, there could be a significant increase in the catch of skipjack tuna (aku) if the effort were increased, or even with the same effort if the fleet fished somewhat farther offshore. According to an analysis by Uchida (1966) of catches per effective trip (a trip in which skipjack tuna were caught), about 80 percent of the effective trips were made within 20 miles from shore and only 20 percent beyond 20 miles. But the offshore catch per trip averaged 50 percent larger than the inshore in recent years (1961-64). If it can be assumed that the ratio of effective to ineffective trips is the same inside and outside the 20-mile distance[2], and if the ratio of offshore to inshore trips could be greatly increased, or even reversed, a very significant increase in catch would result.

This situation suggests that a number of improvements in bait handling, bait keeping and fish keeping may be necessary; and perhaps even baitless methods of fishing island skipjack tuna should be adopted. The payoff on extra costs requires evaluation by a careful systems study. This study needs to be preceded by pilot testing of each element of supposed improvement. Such testing and subsequent systems analysis of gains to be made by various combinations of elements might include, among other things:

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[2] We understand the statistical system is being improved by including the ineffective trips, so the validity of this assumption can soon be tested.

1) Increase the longevity of bait carried by the boats, by reducing the stress placed on bait fish by present methods of bait handling in transfer from bait net to baitwell.

2) Use forced circulation through the baitwells to reduce the further stress during the fishing voyage.

3) Decrease the time spent baiting, preferably to zero, by providing a separate system for catching and holding bait for supplying the boats.

4) Adopt a baitless type of fishing. The former tests of purse seining were made with cumbersome seines which are now obsolete. It is reported, for instance, that the Norwegians with the new materials now available have developed a light, small, seine that can be set and hauled in about 45 minutes. This, or some variant of it, should be tested on the small rapidly swimming schools of skipjack tuna in the waters around Hawaii.

These things might be accomplished in various combinations (as suggested by systems analysis) in the relatively near future and at modest cost, relative to the possible gains. The gain cannot be computed for lack of data, but should be substantial. For instance, if half the time is now spent catching bait and if this were eliminated, the catch might be doubled.

If our vision is raised beyond the island schools of skipjack tuna, however, to the potentials offered by the massive quantities of skipjack tuna which depart from the eastern Pacific fishery without having been perceptibly reduced by the fishery there, the vision is of gains that could be truly spectacular. All available evidence suggests that the skipjack tuna are headed to the westward and that some travel as far as Hawaii and the Line Islands. Hawaii may well have signal logistic advantages as a base from which to tap this rich resource, once we find out more precisely the areas that skipjack tuna favor, and how to catch them economically. If we use the lowest estimate of potential catch of 140,000 metric tons and if a fleet based in Hawaii were only to capture a one-fourth share, her skipjack tuna landings would be over sevenfold the present average tonnage.

To be sure, these are only estimates and verification awaits the establishment of a fishery on this stock of fish which has so far eluded present fisheries. It is unlikely that conventional gear, conventionally deployed, will be effective in fishing this stock. If this were not so, the fishery by this time would have spread naturally to the wider areas the skipjack tuna inhabit.

At this juncture in fishery development we are faced with a series of questions concerning those elements of the skipjack tuna population not now being fished:

1) Where in the approximately 30 million square miles lying south, west, and east of Hawaii and west of the American coastal fishery are the skipjack tuna found in commercially fishable concentrations?

2) Wherever these concentrations may be, are they at the surface or at deeper levels?--or, as is probable, are they sometimes at the surface and sometimes deeper? If so, do they appear at the surface frequently enough for a paying fishery?--and again if so, does this take place in certain physical or chemical oceanographic conditions?--or with certain feeding conditions?

3) Wherever the fish may be, are they collected in small schools, large schools, or scattered? Or are they aggregated variously depending on time of day, season of the year, or some combination of

oceanographic and feeding conditions occurring regularly or sporadically?

4) In whatever state of aggregation they may be, is their state of behavior such that they can be surrounded in a round-haul type of net, or scooped up by a trawl, or entangled in a gill net, or taken on baited hooks, or captured by none of these methods?

To answer these questions, or enough of them to promise some chance of gaining useful information from commercial-scale fishing tests, we need to gain more information on the fish, on the ocean environment the fish inhabits, and on the reaction of the fish to the ocean environment when conditions are in their approximately typical state and when they depart significantly from their typical state.

Without such information a commercial-scale test would not produce useful results. In the unlikely event that such a test succeeded in catching skipjack tuna, it would not be known whether the success could be repeated regularly or only irregularly; and it would not suggest whether or not such successes could be won in any other part of the 30-million-square-mile area or in any other part of the year. In the more likely event that the test failed, it would not be known whether or not skipjack tuna were in the trial area, whether or not the gear was deployed at a different level than was usually occupied by the fish, or whether or not the gear was simply eluded by the fright response of the fish, etc.

About the fish we need to know:

1) Vertical and horizontal distribution according to size, time of year, time of day; and tendencies to concentrate according to conditions of temperature, salinity, oxygen content, abundance of various kinds of food organisms, and probably other physical, chemical, and biotic conditions, all of which tend to have characteristic distributions according to location and season of the year, but which often vary significantly from their characteristic distribution.

2) Schooling behavior, and how it varies with size or age and maturity of the fish, with time of day, time of year, geographic area, and the degree of stability of schools under various conditions, and as modified by internal drives such as feeding, spawning, and migration.

3) Swimming speeds in the undisturbed and excited states, and when migrating.

4) Sensory abilities for seeing, hearing, smelling, tasting, and other stimuli.

5) Feeding behavior, especially as to daily and other periodicities and as to the stimuli by which they locate food.

6) Reactions to fishing gear and other unnatural objects, as to whether they attract or frighten, what modifications heighten attraction and what ones reduce fright, and whether or not the alertness of the fish differs within and between day and night.

About the environment we need to know:

1) The conditions of temperature, salinity, oxygen content, and concentrations of food organisms and other physical, chemical, and biotic properties that prevail in the various ocean areas and at the various depths from the surface down into the thermocline and how these items vary by area and by season.

2) The persistence or variability of these features by short and long time scales, and their relation to the distribution, spawning success, and survival of skipjack tuna larvae.

3) Ocean currents, their direction, velocities, mass transports, and seasonal variations, both on small and

large space and time scales.

About fishing gear we need to know:

1) Its conformation when deployed.

2) The time constants for steps in deployment.

3) Its visibility to skipjack tuna.

4) If drawn through the water, the hydrodynamics of flow through and around the gear relative to speed.

5) Perhaps other characteristics.

These "needs to know" are not stated in order of priority or of importance. Some research is proceeding on most of these subjects at one or another of the fishery and oceanographic laboratories of the world, and advancement of understanding has reached different levels on each subject. The magnitude of the research effort and the order in which various research projects are initiated and completed will be determined by the leads opened up by the research in progress, the hypotheses formulated for test, the advances in technology of instruments and instrument systems, the financial support available, and similar considerations.

This assortment of subjects has a diversity which calls for multidiscipline research. It also calls for observations and experiments at sea and ashore under controlled conditions on live skipjack tuna. To progress most surely and rapidly, the two lines of work should be parallel, with findings from the laboratory tested against observations at sea and deductions from observations at sea tested on live fish in captivity. The laboratory scientists and sea-going scientists working together with constant inter-stimulation will surely evolve more promising ideas and more quickly drop useless ones than would either group working separately.

Although priorities cannot be soundly assigned in advance, the scientific administrator needs to be selective in allocation of effort. We suggest three highly promising courses which should be followed simultaneously:

1) Oceanographic investigations which would bring to light certain features which in some instances have been found to support or to collect organisms of trophic levels below that of the tunas, and to establish the seasons of their formation and dissolution if they are seasonal events, or if they are semi-permanent, to establish the direction and amplitude of their oscillations.

Such features are:

a) Current boundaries and water mass boundaries.
b) Divergences and convergences.
c) Upwellings.
d) Areas of "swarming" of plankton organisms and their downstream successors.
e) Other loci of oceanographic events thought to be conducive to tuna concentration.

2) Paralleling these oceanographic investigations should be experimental work on captive skipjack tuna to test the hypotheses regarding the processes that influence the fish to congregate in certain situations and the senses and reactions involved in their doing so.

3) Another category of research which is greatly needed for judging priorities among sea areas to research for skipjack tuna with the intent of increasing the yield significantly is the subpopulation structure of this species in the Pacific. It has already been established that subpopulations exist, and from other evidence it appears that a most important subpopulation may be the one already supporting the eastern tropical Pacific fishery and probably extending westward

over vast reaches of the tropical Pacific, including the Hawaiian archipelago and waters even farther to the west. Intelligent planning of research and development for extending the fisheries through these waters would be greatly aided by:

a) Establishing the genetic relations between skipjack tuna of the eastern and central Pacific by using samples from the existing fisheries in the eastern Pacific and at Hawaii to investigate immunogenetically.

b) Extending the investigation in the east from California to Peru and in the central Pacific from Hawaii to the Society Islands.

c) As opportunity affords, extending the study also to the island-free waters between the American coastal fishery and the central Pacific, and to the numerous island archipelagoes in the western, central, and far western Pacific.

In the western Pacific a relationship may exist between the skipjack tuna in Japanese home waters and those of the Palaus and other western archipelagoes analogous to that between the eastern and central Pacific. It would be highly desirable to investigate this relationship simultaneously and in about the same order as listed above for the eastern and central Pacific. Cooperation from Japanese laboratories should be forthcoming, at least in collecting the samples from the areas fished by the Japanese skipjack tuna fleet.

INCREASING THE YIELD

To increase the yield of existing fisheries and to promote rapid growth in newly established fisheries there is needed:

1) Improvement of existing fishery statistics (including biological sampling of catches) and establishment of statistical systems for new fisheries. These are essential for efficiently applying population-dynamics analysis to the problem of estimating potential yields and recognizing the approach to the maximal sustainable yield.

2) An understanding of processes that affect the availability (accessibility and vulnerability combined, as defined by Holt, 1960) sufficient for predicting the changes in abundance and location of concentrations of skipjack tuna. This would serve the purposes of (a) increasing the efficiency of the fishery by reducing the time spent ''looking for'' skipjack tuna instead of catching them, and (b) screening out the ''noise'' which renders population dynamics estimates uncertain.

Among the means needed for acquiring information leading to increasing the yield are:

1) Adequate financial support for existing programs of laboratories and starts on new programs.

2) Use of advanced instruments and instrument systems for studies at sea of the horizontal, vertical, and aggregational distribution, and of behavioral responses of skipjack tuna toward fishing gear; it is mandatory to add to conventional instrumentation and sampling gear, means of observing with higher resolution and less distortion. Advanced sonar systems, now being developed for the purpose, offer promise of early availability of instrument systems partially fulfilling this need. More effective fulfillment awaits the availability of high-speed and highly maneuverable submarines. These vessels may be re-

quired even for optimal deployment of the advanced sonar system.

3) For reaching understanding of processes sufficient for predicting changes in abundance and location of concentrations of skipjack and other tunas, there needs to be (a) improvement in the atmospheric monitoring system, especially in the tropical and subtropical Pacific and (b) creation of an equivalent ocean monitoring system to provide data with time and space continuity to depths of at least 500 m., and preferably deeper, throughout the tropical and subtropical Pacific. Such a system would consist of a basic network of ocean stations (deep-anchored automatic, instrumented telemetering buoys) equivalent to the land network of weather stations, supplemented by data from specially instrumented ships-of-opportunity, from overflights by airplanes instrumented with infra-red radiation thermometers and from orbiting instrumented satellites.

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Oyster Setting in Two Adjacent Tributaries of Chesapeake Bay

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The setting of the eastern oyster, *Crassostrea virginica,* was monitored weekly and seasonally for 5 years, 1961 to 1965, in Broad Creek and Tred Avon River on the eastern shore of Chesapeake Bay, Talbot County, Maryland. Data on time of spawning, length and peak of setting season, first season growth and survival of spat, preference of metamorphosing larvae to surface angle, and associated fouling organisms are presented and discussed.

Each year setting was considerably greater in Broad Creek than in the Tred Avon River. The reasons for the higher setting intensity in the creek are not known, though several aspects such as larvae abundance and water quality were investigated.

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THE GROWTH AND MORTALITY OF SEED OYSTERS, *CRASSOSTREA VIRGINICA*, FROM BROAD CREEK, CHESAPEAKE BAY, MARYLAND, IN HIGH-AND LOW-SALINITY WATERS

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ABSTRACT

Seed oysters from low-salinity water of Broad Creek were transferred and suspended off bottom in the low-salinity water of Tred Avon River and high-salinity water of Chincoteague Bay. Growth and mortality were measured and compared for two years. The rate of shell growth was similar in both areas. A high second-year mortality was observed in Chincoteague Bay which apparently was not caused by high salinity.

INTRODUCTION

Certain natural bars in Chesapeake Bay are set aside by the State of Maryland for production of seed oysters, *Crassostrea virginica*. Clean shells, either from shucking houses or dredged off the bottom, are placed on these preserves each spring just before the oyster-setting season. In the fall or early the following spring, the shells with newly attached oysters, called spat, are moved to natural oyster bars. Approximately three years later, after the oysters have reached the 3-inch legal size, they are dredged or tonged and sold by oystermen.

One of the most important seed-producing bars in the Maryland portion of Chesapeake Bay is on the Eastern Shore, at Mulberry Point in Broad Creek. (In 1963 and 1964, for example, 297,420 and 205,460 bushels of shells were planted on this bar to catch seed oysters.) Little is known about the growth and mortality of seed oysters from Broad Creek after they are moved, although Beaven (1952) reported on the growth of seed oysters from several other bars in Chesapeake Bay. Annual surveys by the Maryland Department of Chesapeake Bay Affairs provide information on the density of oysters on many natural bars, but it is difficult to evaluate the growth or survival rate of recently planted seed oysters, since they are usually mixed with other year classes already on the bar.

This paper reports on the growth and mortality of Broad Creek seed oysters of the 1960 year class after their transfer to both the relatively low-salinity water of the Tred Avon River and the high-salinity water of Chincoteague Bay. These areas represent two distinctly different types of environment within the region where seed oysters from Broad Creek could be planted. The salinity is similar at Broad Creek and Tred Avon River; it fluctuates from 8 to 16 ppt (average about 12 ppt). In Chincoteague Bay salinities range from 17 to 35 ppt (average 30 ppt). Seasonal temperatures in both areas vary from 0° to 30° C.

MATERIALS AND METHODS

Samples of seed oysters of the 1960 year class were collected in March 1961 from Mulberry Point, Broad Creek, Maryland (76° 15′ W, 38° 45′ N) On 28 March a portion of the sample was strung on stainless steel wires (50 oysters per wire) and suspended above the bottom from a stationary platform in the Tred Avon River, Oxford, Maryland (76° 10′ W, 38° 41′ N). On 7 April a second portion of the sample was divided into two groups. One group of approximately 250 oysters was placed in a tray 40 inches long, 20 inches wide, and 4 inches deep; a second group of 100 was divided equally and strung on two stainless steel wires. Both the tray and strings were suspended from a tray rack (Castagna, 1964) in Chincoteague Bay at Franklin City, Virginia (75° 23′ W, 38° 0′ N).

Growth of oysters in both localities was measured monthly (except during winter). Growth was determined by an increase in shell height (greatest dorsoventral distance) and length (greatest anteroposterior distance). Initially at Chincoteague Bay, only the oysters on the strings were measured. On 4 August 1961 one string was missing, how-

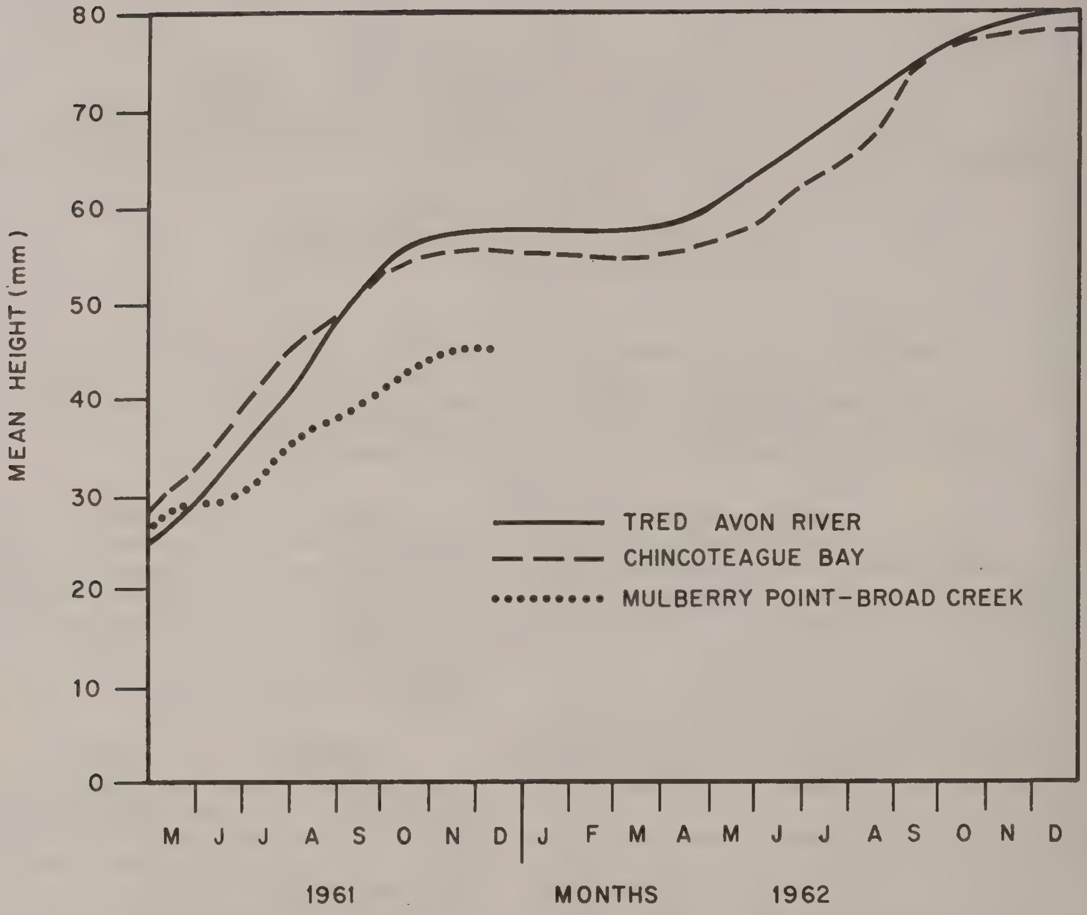

FIG. 1. *Growth curves for Broad Creek oysters suspended off the bottom in the Tred Avon River, Maryland, and Chincoteague Bay, Virginia, and on the bottom at Mulberry Point, Broad Creek, Maryland.*

ever, and on 6 October 1961 the second string was lost; it then became necessary to measure the growth of oysters in the experimental tray. During 1961, samples of seed oysters were also collected periodically from Broad Creek at Mulberry Point and their growth was compared with the growth of oysters suspended off the bottom in the other two areas.

Total counts of live oysters in each stock were made monthly to determine the number of oysters surviving. At the end of the study, on 20 and 28 December 1962, 20 oysters from each group were sacrificed and their per cent solids (Engle, 1950) and index of condition (Grave, 1912; Higgins, 1938) were measured.

GROWTH, SURVIVAL, AND CONDITION OF OYSTERS AFTER TRANSFER

Several investigators have studied the effects of transferring oysters into a new environment. Shaw and McCann (1963) observed that oysters moved from Long Island Sound, Connecticut, to Cape Cod, Massachusetts, grew as well as native populations. Beaven (1952) found that, in general, seed oysters grew best when transferred to nearby waters.

Extensive studies have been carried out on the growth and survival of South Carolina oysters which have been planted in Chesapeake Bay.

TABLE 1. *Mean height, length, and percentage mortality on different dates after transfer from Broad Creek to the Tred Avon River.*

Date	Number Measured	Height (mm) Mean	Height (mm) Standard Error	Length (mm) Mean	Length (mm) Standard Error	Cumulative Mortality (%)
1961						
May 1	102	25.5	0.60	19.9	0.48	0
June 2	101	30.2	0.67	24.2	0.53	0
July 5	101	36.6	0.67	29.3	0.57	0
July 31	100	41.3	0.75	33.7	0.59	3
Sept. 1	100	47.3	0.79	37.8	0.60	7
Oct. 3	100	54.0	0.89	42.1	0.70	14
Nov. 3	100	57.3	0.89	44.6	0.70	14
Dec. 1	100	55.2	0.86	43.3	0.74	14
1962						
April 18	100	57.8	0.57	45.4	0.77	34
May 15	100	61.2	0.94	50.2	0.87	38
June 19	101	64.7	0.97	53.9	0.87	38
July 19	100	67.4	0.99	54.7	0.90	38
Aug. 16	100	71.5	1.03	56.3	0.88	38
Sept. 13	101	73.1	1.04	56.8	0.90	38
Oct. 16	101	77.8	1.14	57.9	0.86	44
Nov. 14	101	78.7	1.13	57.8	0.90	44
Dec. 27	100	80.1	1.12	57.8	0.85	44

Beaven (1953) found that the survival of these oysters was higher in the southern than in the northern portion of Chesapeake Bay. Andrews and McHugh (1957) observed that the growth of South Carolina oysters was almost equal to the growth of native Virginia stocks, but the rate of survival of the southern oysters was lower during the colder seasons from November to May.

In Figure 1 the growth curves are shown for Broad Creek oysters in the Tred Avon River and Chincoteague Bay from May 1961 through December 1962, and at Mulberry Point from May to December 1961. The growth of suspended oysters was approximately the same in the low-and high- salinity waters. By the end of 1961 the oysters averaged 55.2 mm in height and 43.3 mm in length in the Tred Avon River (Table 1), and 56.1 mm and 39.1 mm in Chincoteague Bay (Table 2). At the end of the experiment in December 1962, the average heights and lengths were 80.1 mm and 57.8 mm in the Tred Avon River, and 77.9 mm and 54.8 mm in Chincoteague Bay. Statistical analyses based on methods given in Hubbs and Hubbs (1953) revealed that the small difference in growth between the two areas was not significant.

The growth of oysters on the bottom at Mulberry Point was considerably slower than growth of stocks which were suspended off the bottom (Fig. 1). The average shell height in December 1961 was 11 mm less for oysters at Mulberry Point than for the two suspended stocks (Table 3). Similar results were reported by Shaw (1962) for Cape Cod, Massachusetts. (Since seed oysters are moved by the State from Mulberry Point to other areas, only one year of comparison was possible.)

Little mortality was observed during 1961 at Chincoteague Bay. The survival rate continued high until May 1962, when 34 per cent of the transferred oysters were found dead; by December, when the study was terminated, 74 per cent of the original population had died. Total mortality for the two years was about 44 per cent for oysters in the Tred Avon River; one-half of the deaths in the river were caused by a winter kill which occurred when some of the oysters on the strings were exposed to freezing air temperatures at low tide. It can be assumed that the other half died from natural causes.

On 20 and 28 December 1962, index of condition and per cent solids were determined for 20 oysters from each group. The index of condition was 13.3 and per cent solids 16.4 in Chincoteague Bay; comparable values for oysters in the Tred Avon River were 13.4 and 18.0.

POSSIBLE CAUSES OF MORTALITY IN CHINCOTEAGUE BAY

The effects of moving oysters from low- to high-salinity water was the first factor considered as

TABLE 2. *Mean height, length, and percentage mortality on different dates after transfer from Broad Creek to Chincoteague Bay.*

		Height (mm)		Length (mm)		
Date	Number Measured	Mean	Standard Error	Mean	Standard Error	Cumulative Mortality (%)
1961						
May 2	100	28.6	0.65	21.2	0.49	—
June 1	100	32.8	0.57	24.9	0.49	—
July 3	100	39.4	0.72	29.6	0.62	—
Aug. 4	49	46.3	1.32	35.9	1.08	—
Sept. 5	36	48.6	1.60	36.7	1.33	—
Oct. 6	100	53.4	0.95	38.9	0.59	—
Oct. 31	100	55.3	0.99	40.0	0.64	2.8
Dec. 5	100	56.1	1.03	39.1	0.59	9.3
1962						
May 2	100	56.2	0.94	40.6	0.66	34.0
June 13	100	59.2	0.99	42.4	0.60	50.0
July 12	90	62.8	0.97	44.9	0.65	58.1
Aug. 15	81	67.1	1.04	48.1	0.74	62.3
Sept. 19	76	75.3	1.11	53.3	0.74	64.6
Oct. 18	74	77.4	1.12	55.5	0.77	65.1
Nov. 16	75	77.4	1.12	54.8	0.78	65.1
Dec. 18	55	77.9	1.48	54.8	0.96	74.4

1/ One string of oysters lost.

2/ Second string of oysters lost; measured in tray stock.

a possible cause of death in Chincoteague Bay, but since the greatest mortalities in the Bay occurred during the second year, it does not appear that a sudden salinity change was the cause of mortality. Loosanoff (1950) transferred oysters from low salinities (between 3.0 and 10.0 ppt) directly to water of high salinity (about 27.0 ppt). In general, he observed that oysters withstood sharp changes from low to high salinity without serious physiological effects. Galtsoff (1964) observed total mortality of oysters 3 to 4 weeks after they were transplanted in September from the low salinity (10 to 12 ppt) of upper Chesapeake Bay to the high salinity (32 to 33 ppt) of Sinepuxent Bay at the northern end of Chincoteague Bay. Similar transfers succeeded in October and November, when the air and water temperatures were much lower. He believed that the sudden change in salinity during hot weather was the cause of mortality.

In recent studies at the Oxford Laboratory, little mortality was observed when oysters were transferred from low to high salinity during either cool or hot weather. The oysters were moved from Harris Creek (an area adjacent to Broad Creek) into Chincoteague Bay during March, June, September, and December.

Chincoteague Bay is heavily infested with two serious oyster predators — the Atlantic oyster drill, *Urosalpinx cinerea*, and the thick-lipped drill, *Eupleura caudata*. In the present study, however, the oysters were suspended off the bottom, out of reach of these enemies. Though an occasional drill has been found in adjoining trays, no drills nor drilled oysters were found in the tray holding the Broad Creek stock; thus predation apparently was not the cause for the higher mortality in Chincoteague Bay.

The haplosporidians, "MSX" (multinucleate-sphere x) and *Haplosporidium (=Minchinia) costalis* have been found in the high-salinity waters of Chincoteague Bay (Wood and Andrews, 1962). It is possible that some of the mortality was due to these parasites. To date, neither of these forms has been found in the lower salinity waters of the Tred Avon River.

Until the cause of the high mortality is known and controlled, it appears unwise to transplant stocks of seed oysters from Upper Chesapeake Bay into Chincoteague Bay.

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TABLE 3. *Mean height and length of oysters living on the bottom at Mulberry Point, Broad Creek, on different dates in 1961.*

Date	Number Measured	Height (mm) Mean	Height (mm) Standard Error	Length (mm) Mean	Length (mm) Standard Error
May 10	100	27.6	0.50	20.2	0.39
June 6	100	29.2	0.76	21.1	0.52
July 6	100	31.2	0.61	23.5	0.51
Aug. 1	100	35.6	0.73	25.6	0.51
Aug. 29	100	39.0	0.69	26.8	0.50
Sept. 26	98	40.7	0.67	28.1	0.46
Nov. 7	100	44.4	0.71	31.7	0.50
Dec. 7	100	44.8	0.71	31.1	0.49

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WILY OYSTERS OUTWIT ENEMIES

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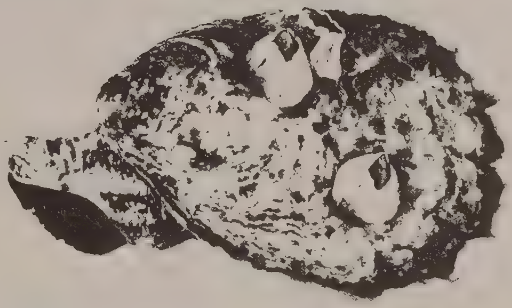
Oysters are found attached to a variety of things. In addition to shells, oysters attach themselves to rocks, bottles, shoes, rubber tires, pilings, buoys, hulls of boats, and many other submerged objects located where oyster larvae undergo metamorphosis. In two rare situations reported here, oysters were attached to the shell of two of their enemies—the eastern oyster drill, and the blue crab.

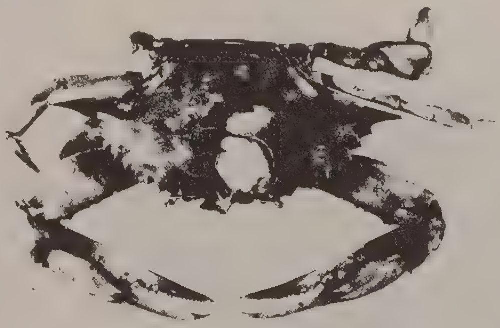
The first observation was made by Walter Dahlstrom, marine biologist for the California Department of Fish and Game. Mr. Dahlstrom found an Olympia oyster attached to the shell of a live oyster drill in San Francisco Bay near Redwood City (Fig. 1).

In the second unusual case, a blue crab was caught by William Cottingham in the Tred Avon River, Oxford, Maryland. On top of the crab's back were two young oysters (Fig. 2), respectively.

These observations represent two rare occurrences in that the oysters were attached to live specimens. Occasionally oysters have been found on the shells of dead snails. By attaching to the shell of the drill and crab, the oysters had escaped predation by these two enemies and from other predators in the area.



An Olympia oyster attached to the shell of a live oyster drill.



Two young oysters attached to the back of a blue crab.

Proceedings of the National Shellfisheries Association
Volume 56 — May 1966

SETTING AND GROWTH OF THE AMERICAN OYSTER, *CRASSOSTREA VIRGINICA*, ON NAVIGATION BUOYS IN THE LOWER CHESAPEAKE BAY

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BIOLOGICAL LABORATORY
OXFORD, MARYLAND

ABSTRACT

Samples of oysters were collected for 7 years from selected navigation buoys, moored in the lower Chesapeake Bay from the mouth of the Potomac River to Cape Charles, to obtain data on oyster growth and mortality. The shells of the live oysters were measured, year classes separated, and an average rate of growth determined. Indexes of mortality were estimated by counting dead oyster valves attached to the buoys.

Average ranges of shell height were 25 to 35 mm at the end of the setting year; 70 to 80 mm by the end of the first year; and 80 to 95 mm by June of the second year (buoys are generally on station a maximum of 2 years). This growth is extremely rapid, apparently the result of being off-bottom. Not only was growth rapid, mortalities were unusually low on the buoys.

The extensive setting of oysters on navigational buoys, followed by rapid growth and low mortalities, suggests the commercial possibilities of off-bottom culture of oysters in certain areas of the lower Chesapeake Bay.

INTRODUCTION

Buoys used as navigational aids are placed at vantage points along practically all coastal and large inland waterways. They are brought ashore to Coast Guard bases periodically for cleaning and servicing (Fig. 1). Any biological material attached to the buoys while they are "on station" is available for collection and study (Merrill, 1965). Not only is material from buoys easily attainable but each buoy has its own community structure. Because buoys are on station for known periods of time, growth of the animals collected from them can be interpreted.

Growth of various bivalves from buoys has been studied over the past few years. In the sea scallop, *Placopecten magellanicus*, for instance, only occasional very young specimens are taken in their natural habitat (Merrill, 1965). Most of what is known of this scallop's early rate of growth has been learned from collections taken from many buoys in the New England area. Galtsoff and Merrill (1962), who studied *Ostrea equestris* using material collected from an ocean buoy off Georgia, determined, among other things, a rate of growth for this species in surface waters. Merrill (1959) reported an unusually fast growth of the soft-shell clam, *Mya arenaria*, which had settled and nestled in a thick hydroid growth far up in the

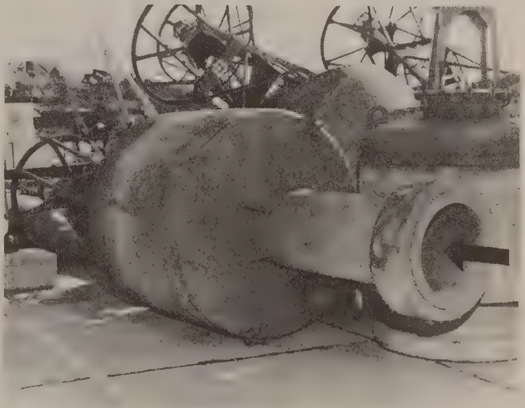


FIG. 1. *Navigation buoy; arrow indicates the sheltered inner portion of the stabilizer tube from which oysters were taken.*

stabilizer of a navigation buoy at Buzzards bay, Massachusetts.

Study of the growth of bivalves from surface buoys is tantamount to the study of growth from raft culture. Reports have shown that growth is faster nearer the surface than on the bottom. Belding (1916) reported faster growth for soft-shell clams suspended from rafts than for those in boxes buried to the level of the substrate; in Europe, where farming of the mussel, *Mytilus edulis,* is practiced extensively, growth is faster in those cultivated on wooden frames above the sea bottom. Studies by Shaw (1962, 1964, 1965) have shown that the American oyster, *Crassostrea virginica,* grows almost twice as fast when suspended from rafts as on the bottom. Bonnot (1935) and Quayle (1956) stated that the culture of Pacific oysters, *Crassostrea gigas*, from rafts greatly increased the growth of the suspended oysters. Quayle (1956) further determined that oysters cultured by this method show lower mortality because of elimination of silting and reduction of predation. Belding (1930) considered the most important factor in the growth of clams to be a good current which carries food, oxygen, and salts; this current also acts as a sanitary agent.

The purpose of this paper is to describe the results of a study of the growth and mortality of *Crassostrea virginica,* which had settled and grown on navigation buoys near the water surface. An evaluation is made on the possibilities of developing off-bottom culture of oysters in these waters.

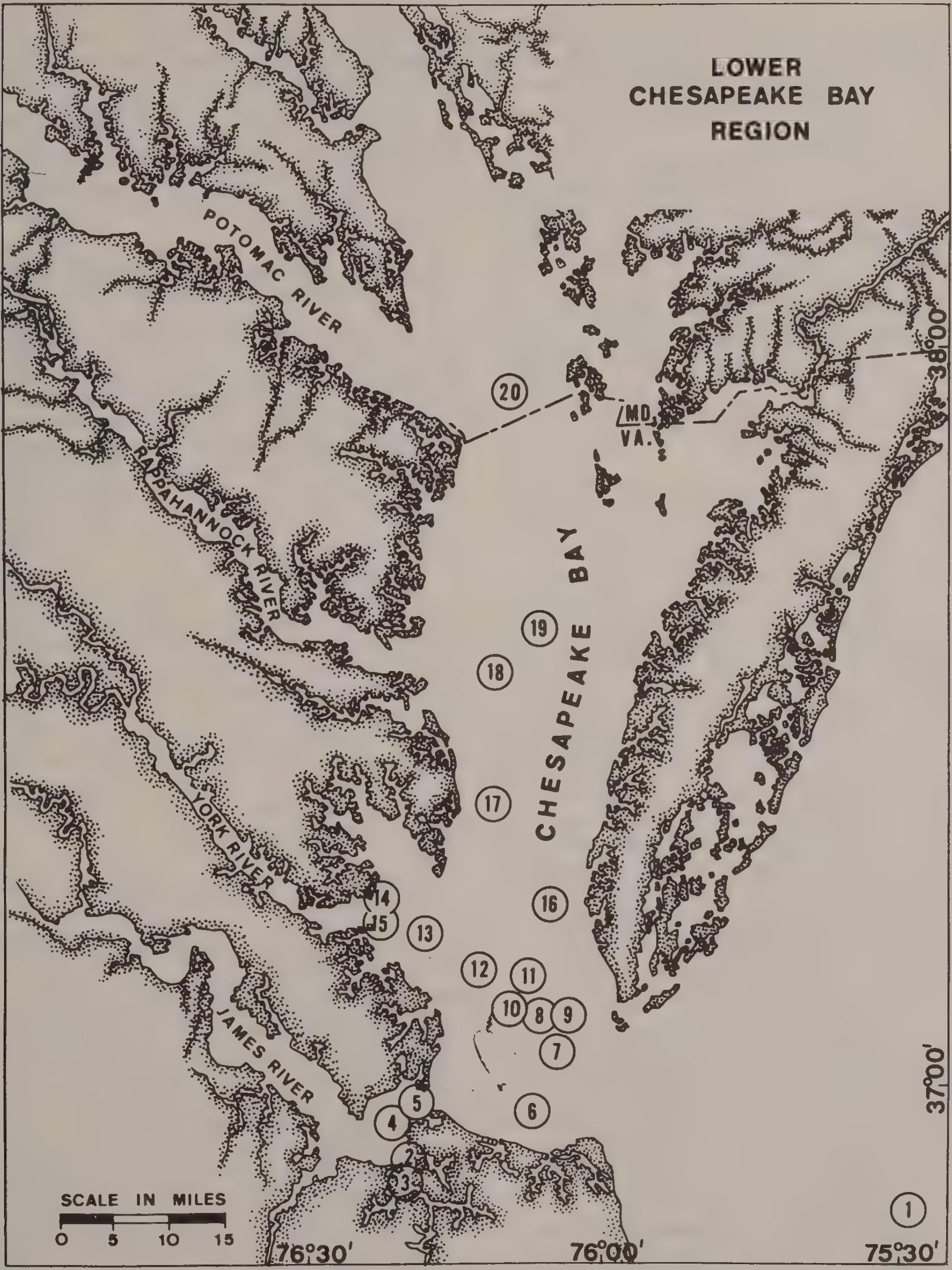
PROCEDURE

The Coast Guard keeps accurate records for all buoys — when and where they are placed on station, and when they are brought ashore for cleaning (Table 1). It was from these buoys that we collected our samples.

Oysters were taken from selected navigation buoys for 7 years at the Portsmouth, Virginia, Coast Guard Base. These buoys had been moored in the lower Chesapeake Bay from near the mouth of the Potamac River to Cape Charles (Fig. 2). All live oysters were collected from at least 50 square feet of the inner tube surface; we also removed the oysters over 30 mm (which could be seen easily) that had died but whose valves or under-valves remained attached to the buoy. These dead oysters were counted to determine indexes of mortality. Height (greatest dorsoventral distance) of 1,536 oysters from 20 buoys (an average of 79 specimens from each buoy) was measured. Size frequencies were established and then, with the aid of probability paper, year classes were separated and the mean height for each year class determined (see Harding, 1949). Comparison of mean heights of oysters from most northern and most southern

TABLE 1. *Location of buoys, date of placement and retrieval, and number of live oysters collected from each buoy. Location numbers correspond to those in Figure 2.*

Location					
Number	Latitude N.	Longitude W.	Date In	Date Out	Number of oysters
1	36°51.5′	75°30.0′	5-22-58	7-25-60	77
2	36°53.6′	76°20.0′	1-14-60	5- 2-62	55
3	36°53.6′	76°20.0′	5- 2-62	4-27-64	36
4	36°58.2′	76°20.0′	8- 9-60	8-16-62	85
5	36°59.2′	76°18.8′	12-19-61	8-27-63	70
6	36°58.7′	76°07.5′	11-20-59	11-21-62	45
7	37°04.3′	76°04.8′	4- 7-58	5-19-60	45
8	37°12.0′	76°08.5′	1- 2-60	10-31-61	18
9	37°07.0′	76°07.8′	4-19-61	8-18-62	7
10	37°07.4′	76°09.2′	11- 4-57	10-10-59	92
11	37°09.4′	76°08.5′	8-21-59	12-15-61	115
12	37°08.7′	76°11.5′	6-28-56	5-28-58	104
13	37°13.5′	76°08.4′	2-28-62	11- 1-62	17
14	37°15.0′	76°22.6′	5-28-58	5-19-60	190
15	37°15.0′	76°22.6′	5-19-60	5-22-62	181
16	37°15.0′	76°07.0′	10- 6-59	10-19-61	77
17	37°23.5′	76°11.5′	10-10-60	10- 9-62	25
18	37°34.5′	76°10.4′	10- 1-62	6- 8-64	94
19	37°38.8′	76°07.5′	12-10-61	6- 8-64	50
20	37°59.4′	76°10.9′	6- 5-58	9- 5-60	58


LOWER
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REGION
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RAPPAHANNOCK RIVER
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JAMES RIVER
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FIG. 2. *Lower Chesapeake Bay region showing locations 1-20 of navigation buoys from which samples were collected.*

stations proved the rates of growth to be closely similar. Thus we were able to combine all data and establish an average growth curve for the entire area of lower Chesapeake Bay.

RATE OF GROWTH

Oysters set in lower Chesapeake Bay from June through October (Loosanoff, 1932; Andrews, 1951, 1954). Shell growth takes place from April to November in the Bay, but little or no growth is laid down from December through March (McHugh, unpublished manuscript[1]). The average height of buoy oysters ranged from 25 to 35 mm by the end of the setting year (time of setting to January 1), from 70 to 80 mm by the end of the next year, and 80 to 95 mm by June of the following year. Since buoys are generally in the water a maximum of 2 years, data on later growth were not available.

Comparison of the growth of buoy oysters with that of other experimental stocks grown off the bottom in Chesapeake Bay makes it obvious that the oysters attached to buoys grow faster. As an illustration, the comparison of the growth of oysters collected from buoys with that of Broad Creek seed suspended on ropes in the Tred Avon River, Maryland, can be seen in Figure 3. Comparative measurements for South Carolina and York River seed suspended in trays at Gloucester Point, Virginia, are also indicated. At the end of the setting year a difference in growth rate is already apparent; the buoy oysters averaged 8 mm larger than the Broad Creek stock suspended in the Tred Avon River. By the end of the next year the buoy oysters averaged 15-23 mm larger than the York River, South Carolina, and Broad Creek stocks. In fact, many of the oysters from buoys were 75 mm or greater at the end of 1 1/2 years; some suspended stocks did not attain this height until almost the end of the following year, or 2 1/2 years after setting.

MORTALITY OF BUOY OYSTERS

As mentioned earlier, a count was made of all "boxes" and "scars" for those oysters 30 mm or greater. The number of dead oysters was extremely low. Only 32 scars and boxes were observed; the indicated mortality is about 2 per cent (computed from the total number of oysters examined).

INTENSITY OF SETTING

The number of oysters collected from individual buoys varied from 7 to 190 (Table 1), and average 78.6 per buoy. Among the areas monitored in the lower bay, setting was the heaviest at the mouth of the York River on buoys 14 and 15 (Fig. 2). At this station 190 and 181 oysters were collected from the two buoys. Counts also exceeded 100 oysters on buoy No. 12, 5 miles ENE of Plumtree Point, and on buoy No. 11 in the middle of the Bay off the town of Cape Charles (Fig. 2).

POSSIBILITIES FOR OFF-BOTTOM CULTURE IN LOWER CHESAPEAKE BAY

The rate of growth of buoy oysters was greater to our best knowledge than that of any stock north of Cape Hatteras. This rapid growth is probably the result of currents that bring plentiful food materials (Merrill, 1965). In more protected waters, the reduction of currents lessens the amount of food available to the oysters. The slower growth rate of the suspended stocks in York River and Tred Avon River as compared with those attached to buoys are more than likely related, in part, to the strength of water current.

Currents over the bottom are further reduced, and it is in this zone that oysters grow the slowest. Beaven (1952) observed that oysters growing on the bottom in Holland Straights, Chesapeake Bay, Maryland, grew to only 48 mm in height after 2 years. Buoy oysters reached this size during the first year of growth (Fig. 3).

It is possible that the oysters are not in the water long enough (a maximum of 2 years or less) to be killed by diseases known to be prevalent in these areas (Andrews, 1964). It would be worth a study to check the incidence of the common oyster disease organisms in large oysters from buoys.

The fact that the height of buoy oysters averaged 80 to 95 mm after only 2 years of growth, and the apparently low mortality among these oysters warrants, in our opinion, further investigations into the possibilities of developing off-bottom culture in certain areas of the lower Bay.

One site worth considering is the mouth of the York River, where setting was the heaviest on the buoys. Shells could be suspended from rafts moored in this locality. Following setting, the rafts could remain at the site until November when growth for the season has terminated. They could then be towed to more protected waters for the duration of winter to shield the oysters from floating ice and storms. The following spring the rafts could be moved to more open waters in order to take advantage of faster currents and increased amount of food materials which contribute to oysters' faster growth. This method of culture is similar to that now being conducted so successfully in Japan.

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[1] McHugh, J. L. (unpublished manuscript), "Growth of oysters at Gloucester Point, Virginia."

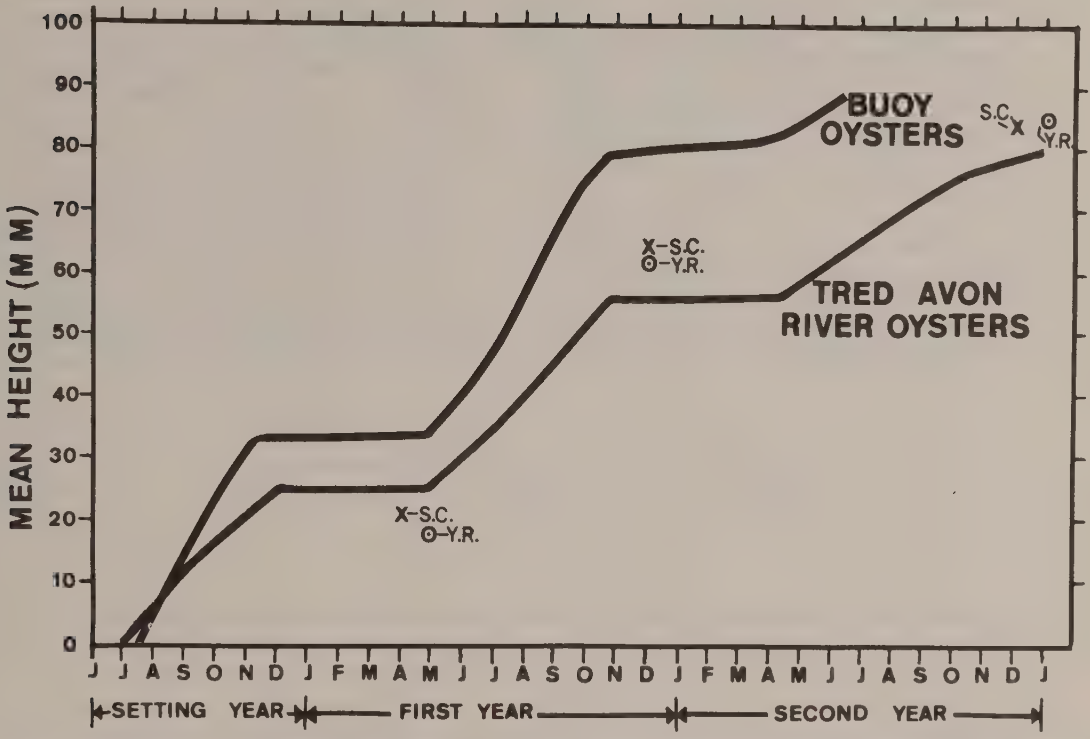

FIG. 3. *Growth of buoy oysters and Tred Avon River oysters. Measurements of tray-held York River and South Carolina oysters are indicated by O-Y.R. and X-S.C.*

CONCLUSIONS

The continuous decline of oysters in Chesapeake Bay, and more recently, the rapid loss of oysters in the lower Bay from diseases and predation, necessitate a close look at present-day culture techniques. The collections from buoys suggest that suspended culture may be one means of supplementing production of a declining industry. Although this method of culture increases costs, the present scarcity of oysters in turn increases the value of the product. In areas where off-bottom culture has been studied, faster growth and greater survival has been found in comparison with oysters grown on the bottom. Oysters grown off-bottom can be marketed earlier than similar stocks growing on the bottom. Also, the lower mortality among suspended oysters means the marketing of greater volumes.

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p. 24

FREEZE-DRYING AS A STANDARD METHOD FOR TOTAL SOLIDS IN SHELLFISH

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(ABSTRACT)

Lyophilization or freeze-drying is being used at this laboratory to determine the percentage of solids (dry weight of meat divided by wet weight of meat, times 100) of shellfish. This method is simpler and faster than conventional oven drying.

In parallel analysis over a 1-year period, the freeze-dry technique (12 hours to process) and the oven-drying technique (24 to 48 hours to process) have given similar results. Other methods of determining the condition of oysters are discussed and evaluated.

Because diverse procedures are being used to measure oyster condition, it is suggested that the freeze-dry technique be established as the standard method.

Copepods of Gulf of Maine Coastal Waters

By KENNETH SHERMAN

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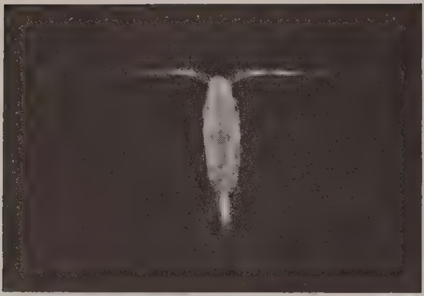
Oceanic food production is dependent on a series of energy-transforming links along a food chain. The basic links are forged by a multitudinous community of minute plants and animals found living in the surface layers of marine waters. This passively-floating community, known collectively as plankton, is constantly occupied with producing and transforming food energy. This energy is transferred, via the gaping jaws of predators, along the oceanic food chain. The plant constituent of the plankton (phytoplankton) is composed of delicate microscopic uni-cellular organisms, which are the producers of the basic food-stuff of the oceans. Bathed by inorganic dissolved nutrients, and energized by solar radiation, these plants synthesize organic food — starches, carbohydrates, fats, and proteins — for the next food chain link, the animal plankton (zooplankton). It is at this vital stage in oceanic food-energy transferral that copepods assume major importance. They graze on the expansive marine pastures of phytoplankton, and convert and concentrate these minute plants into animal substance large enough to be utilized by the larger marine organisms, most of which are incapable of feeding directly on small phytoplankters.

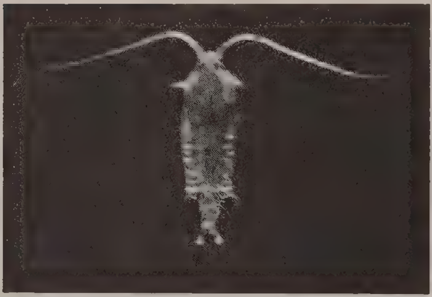
In Maine coastal waters, copepods are among the smallest of crustaceans, ranging from 1 to 4 millimeters long (0.04 to 0.16 inches). However, when one considers numerical abundance, copepods as a group are the dominant members of the zooplankton community. They constitute from 40 percent to 85 percent of the total zooplankton in the upper 20 meters of water. In numbers, they range from a summer high of approximately 15,000 per hundred cubic meters (26,415 gallons) of water, to a winter low of 2,000 per hundred cubic meters of water.

Twenty-two species of copepods occur in Maine coastal waters, of which 14 are found only rarely, generally as immigrants from offshore waters. Eight species — *Calanus finmarchicus, Centropages typicus, Metridia lucens, Pseudocalanus minutus, Acartia longiremis, Oithona similis, Temora longicornis,* and *Tortanus discaudatus* — occur regularly, and of this group *Calanus finmarchicus* and *Centropages typicus* are the most numerous. Photomicrographs showing the differences in body structure and delicate symmetry of these eight copepods are shown in Figure 1.

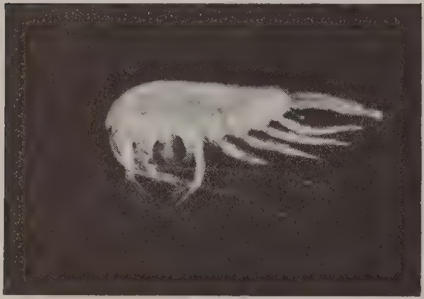
Copepods are uniquely adapted for a planktonic existence. The antennae and caudal hairs (setae) are elongate, and in some Gulf of Maine species spectacularly plumose, thereby providing more surface area and increasing buoyancy. In addition, fat globules, important metabolic products in many species, can be stored to sustain the organism through periods of low phytoplankton abundance, while also effectively increasing buoyancy. The copepod body is composed of two major parts, the wide anterior metasome, and the narrowly elongated



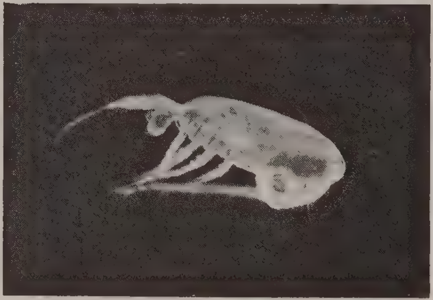
Calanus finmarchicus x6



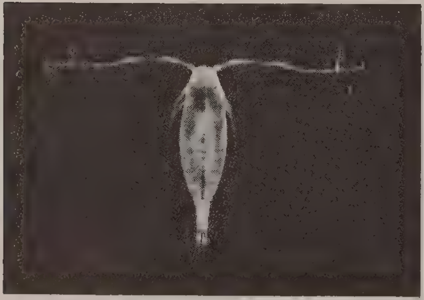
Centropages typicus x13



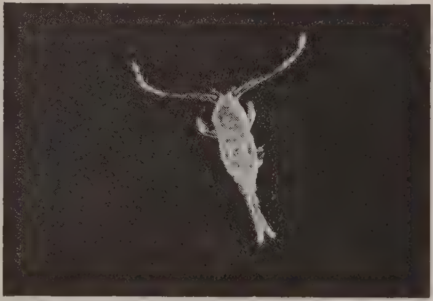
Metridia lucens x16



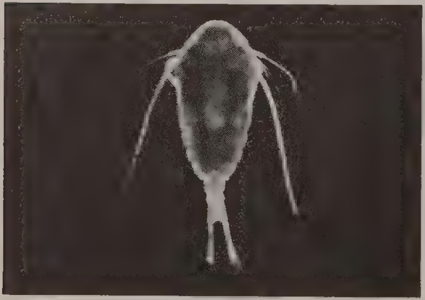
*Pseudocalanus minutus** x23



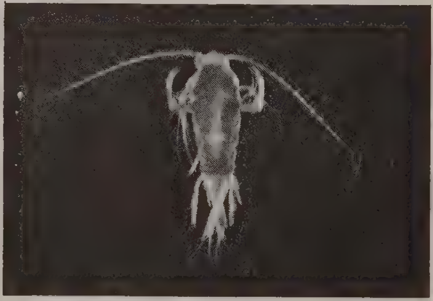
Acartia longiremis x21



Oithona similis x28



Temora longicornis x19



Tortanus discaudatus x12

Figure 1. Photomicrographs of eight commonly occurring Gulf of Maine coastal copepods. Magnification values are given for each species.

**P. minutus*, female with eggs attached to the genital segment.

posterior urosome. Feeding is accomplished by rhythmical movement of five pairs of modified appendages (second antennae, mandibles, maxillules, maxillae, and maxillipeds) arranged on the anterior ventral surface of the metasome. These appendages, when in motion, set up small circular currents about the copepod into which food organisms are drawn. Ultra-small organisms are filtered directly into the mouth area. Other organisms, particularly phytoplankters, are collected with the maxillipeds and compacted into an elongate food pellet, which is then ingested.

Movement is generally directed vertically through the water column, with propulsion resulting from the rapid movement of five pairs of oar-like legs. In some species, this vertical movement assumes a diurnal periodicity, with individuals rising to the surface waters in the evening and descending toward the depths in daylight. Horizontal distribution, however, is limited to the movements of currents and tides, carrying the free-floating copepods considerable distances.

The more prolific species occurring in Gulf of Maine coastal waters — *Calanus finmarchicus* and *Centropages typicus* — dominate the copepod fauna during different seasons, with the former more abundant in winter and summer and the latter more numerous during spring and fall. At least two and possibly three generations of these species are produced annually, each species taking up to three months to develop from egg to mature adult. After hatching from the egg, the individual undergoes two major body-form changes, the earliest of which is the nauplius stage and the later, the copepodite stage. In all, 12 distinct moultings occur — 6 nauplius and 6 copepodite — each characterized by an increase in size and degree of appendage development. The maximum life-span is approximately one year. However, four or five months is the average, as copepods are the main food source for large numbers of Gulf of Maine fish species, particularly the commercially important sardine-size herring. Young herring larvae prey heavily on the early nauplius stages, while the older stages feed on the adult copepods.

In addition to their importance as a food source for herring populations, copepods can be used as indicators of hydrographic conditions. The "type" of marine waters present in a fishing area, whether of oceanic, coastal, or mixed-type can influence the success of the herring fishery. A distinct zooplankton fauna is usually associated with these water types. In coastal areas, where a large degree of vertical mixing occurs, it is difficult to identify intrusions of oceanic water, or of increased outflow of less saline water along the coast. In this situation, copepods have been used as indicators of hydrographic conditions, as they are retained within a body of water long after temperature or salinity changes have occurred.

An outstanding characteristic of copepod populations is their uneven distribution pattern. Whether this is due to uneven reduction in numbers by selective feeding of predators, to differential movements of currents, to swarming during spawning periods, to differences in areal productivity or to a physiological response to the environment, is not presently known. However, this problem of irregular copepod distribution is receiving considerable study by marine scientists, particularly since copepods are so vital a link in the food chain of the oceans.

As part of a research program on immature herring, the Bureau of Commercial Fisheries Biological Laboratory, Boothbay Harbor, Maine, has initiated a study of Gulf of Maine coastal zooplankton, with particular reference to copepods. Research is directed toward providing information regarding seasonal and annual changes in zooplankton distribution and abundance, information which is essential for a more complete understanding of the relations between fluctuations in herring abundance and variations in environmental conditions.

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PACIFIC HAKE FISHERY: A PROGRESS REPORT

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U. S. Bureau of Commercial Fisheries

My purpose is to review the progress that has been made in efforts by various research groups to encourage a fishery upon Pacific hake found off the coast of California, Oregon, and Washington.

The Pacific hake, *Merluccius productus,* a member of the codfish family, is one of a half dozen or so species of the genus which is world wide in its distribution. Hake are found and fished off the coasts of Europe, South Africa, and South America. On the east coast of the United States where hake usually go under the name of "whiting", close to 100 million pounds are landed yearly and are largely utilized for human consumption. World hake landings in recent years have averaged around 400,000 metric tons. What then of hake on the Pacific Coast of the United States?

The general abundance of hake on the west coast of North America has been known to commercial and sports fishermen for many years, and recently some effort at quantifying the extent of the resource has been made. Egg and larval surveys by California Cooperative Oceanic Fisheries Investigations and Bureau of Commercial Fisheries Laboratory at La Jolla, California, have indicated that the Pacific hake ranks second to only the northern anchovy in abundance off California. The size of the standing crop of hake spawning off California has been estimated from eggs and larvae to be in the order of magnitude of 6 billion pounds.

A second means of estimating the quantity of hake is through exploratory fishing in conjunction with echo sounding surveys. This work has been carried out by the Seattle Exploratory Fishing and Gear Research Base of the U. S. Bureau of Commercial Fisheries. The vessel JOHN N. COBB is equipped with a large mid-water trawl developed by the Bureau's Gear Research section. This pelagic trawl has pressure sensing devices that permit the trawl to be fished precisely at any desired depth. It has proved to be very effective on hake when used in conjunction with Simrad echo sounding gear. The trawl has additional advantages in that it can be fished over any type of bottom and takes catches that contain little else than hake.

Explorations by the JOHN N. COBB in 1964 established that large compact schools of hake were present off Washington, Oregon, and Northern California from mid-May until mid-November. Mid-water trawling off Washington and Oregon during this period consistently took catches in excess of 15,000 pounds per ½ hour with a high catch of 60,000 pounds in ½ hour. These explorations suggested that hake were sufficiently abundant along that Washington-Oregon coast to support a commercial fishery during the period when hake were present.

Assuming that the COBB located all of the hake schools off Washington and Oregon and that all fish in front of the trawl were captured, both very conservative assumptions, the standing crop of hake off Washington and Oregon during 1964 was estimated at 1 billion pounds.

Studies of Pacific hake at the Seattle Biological Laboratory of the Bureau of Commercial Fisheries are being conducted as a part of the Groundfish Program, a new area of investigation begun in 1964. The principal objective of hake studies is to provide an assessment of the maximum sustainable yield of hake found off Washington and Oregon to aid in the management of the resource.

Using available information on rates of growth, mortality, and recruitment, biologists at the Seattle Biological Laboratory placed the maximum sustainable yield of the resource off Washington and Oregon at from 100,000 to 150,000 tons per year, enough to support the operation of a moderate size reduction plant during the 6-month period when hake are available. Let me emphasize that this estimate of the maximum sustainable yield is most conservative and assumes that the exploratory sampling effort was 100 per cent efficient. A continuing effort is being made to improve on the accuracy of this estimate Personnel from the Seattle Biological Laboratory accompany the JOHN N. COBB during its hake surveys to collect biological data relating to this objective.

This past summer the Seattle Exploratory Fishing and Gear Research Base continued its surveys for hake along the Pacific Coast. A commercial vessel, the WESTERN FLYER, was chartered for 99 days to simulate commercial fishing on hake off Washington and Oregon. Deliveries were made to a reduction plant located at Warrenton, Oregon near Astoria. During the 62 days of actual fishing activity the WESTERN FLYER took 872 tons of hake. This was much less than was originally anticipated and was caused by an inexplicable scarcity of hake schools in the vicinity of the Columbia River mouth. Nevertheless, the crew of the WESTERN FLYER quickly learned the use of the pelagic trawl with its telemetering system and made 170 drags with the gear. A second commercial fishing vessel, the ST. MICHAEL, was chartered to test smaller versions of the COBB pelagic trawl which may be suited for smaller and less powerful boats than are required to use the full-size gear.

Commercial utilization of hake has been under investigation by Oregon State University and the Seattle Technological Laboratory of the Bureau of Commercial Fisheries. Uses that have been found or suggested for hake include human food, animal food, fish meal and oil, and fish protein concentrate or fish flour. Of these products the most promising use for hake at the present appears to be fish meal. Fish meal has an established market throughout the world, and there is a trend of increasing demand as its use in poultry and livestock feeds continues to grow. Because of a sharp increase in the price of fish meal during the last few years, the economic outlook for this product is much more favorable than in the past.

Hake taken off Washington and Oregon have been found to consist of 15 per cent protein, from 2 to 5 per cent oil, about 2 per cent ash and the remainder, about 80 per cent, moisture. This means that 5 to 6 tons of raw hake are required to produce 1 ton of fish meal. The variable oil content of Pacific hake means that (1) equipment for oil extraction must be provided in a hake processing plant to produce a uniform quality meal and (2) a hake meal industry with a relatively small or non-existent income from oil must be a high-volume efficient operation in order to produce fish meal at a competitive price on the world market.

The fishing industry has shown a keen interest in the development of a hake fishery. If present plans are fulfilled, a new reduction plant should begin the processing of hake on the Washington coast by next spring. It is also likely that one or more hake reduction plants will be operating in California by next year.

The extensive use of Pacific hake as human food is somewhat less promising than its use as fish meal. A common complaint about fresh Pacific hake is that it is soft, bland, and of a watery texture. On the other hand, most of the hake landed on the eastern coast of the United States are accepted as human food so a similar market would appear to be available for Pacific hake. Research on methods of marketing fresh hake products is continuing.

Another potential use for hake as human food is found in fish protein concentrate or fish flour. Hake appears to present no special problem as a source of F.P.C., but development must await the completion of feasibility studies on the east coast as well as clearance of the product by the Food and Drug Administration.

During the past year meetings have been held between State and Federal agencies to exchange information and to develop a systematic approach to hake research. Progress is being made with regard to standardization of measurement and classification of biological data as well as in the collection of uniform catch information. Joint research projects are being planned between Bureau of Commercial Fisheries Laboratories in Seattle and La Jolla.

Effective management of Pacific hake under a commercial fishery poses a complex problem for the state agencies involved. The apparent migration pattern of hake along the Pacific Coast with spawning during the winter off southern California and summer feeding from northern California to southern British Columbia implies that cooperation is needed between the states. The mechanics of such cooperation might well be provided by the Pacific Marine Fisheries Commission. I should like to suggest that a discussion of the management of a Pacific Coast hake fishery be placed on the agenda of the spring meeting of the Pacific Marine Fisheries Commission's Research Staff.

A hake fishing industry, since it is new and involves few or no established interests, offers an excellent opportunity for an experiment in a limited entry fishery. A limited entry fishery[1] might serve as encouragement to fishermen, processors, and investors. Many of the economic problems besetting our established fisheries can be attributed to over entry, and with a budding industry on hake we have a splendid opportunity to manage it properly from the beginning without waiting for problems to develop before initiating management procedures.

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[1] Chairman Woodworth replied,

"Thank you, gentlemen, for your excellent reports. We would like very much to comply with Mr. Shippen's request to limit entry into the hake fishery, but I am afraid that PMFC's compact specifically forbids such compliance.

"The second paragraph of Article I of the compact says: 'Nothing herein contained shall be construed so as to authorize the aforesaid states or any of them to limit the production of fish or fish products for the purpose of establishing or fixing the prices thereof or creating and perpetuating a monopoly.'

"However, PMFC has a proposal, No. 5, before it to establish a program of coordinated management and research for this new fishery."

Reprint In Thomas A. Manar (editor), Proceedings, Governor's Conference on Central Pacific Fishery Resources, State of Hawaii, Honolulu, 1966.

AGE AND GROWTH STUDIES OF FOUR SPECIES OF TUNAS IN THE PACIFIC OCEAN

By

Richard S. Shomura, Fishery Biologist
Bureau of Commercial Fisheries Biological Laboratory
Honolulu, Hawaii

ABSTRACT

Recent studies of the age and growth of tunas in the Pacific Ocean are reviewed and parameters of the von Bertalanffy growth functions estimated if they were not supplied by the original authors. All the basic methods used in the study of age and growth, i.e., rings on hard parts, progression of modal sizes in length-frequency distributions, and tagging data, have been applied to albacore (Thunnus alalunga). The results have varied with methods and also between investigators sampling from the same area. The surprisingly few studies on skipjack tuna (Katsuwonus pelamis) agree fairly well. Estimates of age and growth of yellowfin tuna (T. albacares) from several parts of the Pacific Ocean agree rather closely, as do several studies of bigeye tuna (T. obesus).

INTRODUCTION

The earliest reference to a study of age and growth of tunas has been traced to observations by Greek fishermen about 2,000 years ago (Bell, 1964). These fishermen recognized three age groups in the bluefin tuna catch and noted that a scarcity of the smallest age group in one year was followed by the failure of the fishery the following year. Although this observation suggests an early recognition of the value of age and growth studies in a tuna fishery, it has been only in the last 10 years that a considerable amount of effort has been directed toward this phase of fishery research. Furthermore, much of the recent work has been limited to the stocks of tunas in the Pacific, particularly the North Pacific. To date, no detailed age and growth studies have been undertaken on the commercially important tuna species in the Indian Ocean. In the Atlantic, the few studies thus far have been directed toward bluefin tuna and albacore.

Within the past 10 years two reviews on age and growth of tunas have been published. Hayashi (1958) reviewed studies on age and growth of Pacific tuna stocks published before 1956, and Bell (1964) summarized on a worldwide basis nearly all of the papers on age and growth published before 1962. Rather than make another detailed review of earlier studies, I shall emphasize investigations carried out since

1963, weigh the relative merits of the different methods of aging tunas, and compare the results of various investigators. Different authors use different measures of age, e.g., actual age, size at time of ring formation, and relative age (size at age N, N + 1, etc.). I have attempted to locate a common ground for comparison and the age measure used herein sometimes may differ from that provided by the author. I have also included estimates of the parameters of the von Bertalanffy growth function. For some age and growth studies, in which the authors have used this function to describe the growth of a species, the authors' values are cited. Where estimates of the parameters are not provided in the published works, I have estimated these values, using data extracted from the publications. These parameters were computed by automatic data processing.

ALBACORE

More studies have been conducted on the age and growth of albacore than on any other species of tuna. Whether this situation reflects the high economic importance of this species or the accessibility of sampling material has not been ascertained. Hayashi (1958) and Bell (1964) showed that all three basic methods used in study of age and growth, i.e., rings on hard parts, progression of modal sizes in length-frequency distributions, and tagging data, have been applied to albacore. The results have varied with methods and also between investigators sampling from the same area. This variation is surprising, for a growing body of evidence indicates that a single stock of albacore exists in the North Pacific Ocean (Otsu, 1960).

The most recent study of age and growth of albacore is based on ring counts on scales of fish caught in the northwestern Pacific by longline and pole-and-line gear (Yabuta and Yukinawa, 1963). The authors examined scales from fish sampled at the Tokyo and Yaizu markets over the period 1952-62. Scales from only 658 of a total of 1,895 fish were considered readable. The authors determined the relationship between scale diameter and fish size (fork length) and established the size of fish at time of annulus formation. The results are presented in table 1 and shown in figure 1; here, as in figures 2 and 3, I have assumed, in assigning ages, that annulus formation occurs in northern winter and spawning in northern summer. Data plotted are those of method B, table 1, offset by a half year to express Yabuta and Yukinawa's "number of rings" in my estimates of

Table 1.--Estimated length of albacore from northwest Pacific (adapted from Yabuta and Yukinawa, 1963)

Number of rings (Approximately equivalent to years)	Fork length (cm.)	
	Method A[1]	Method B[2]
1	27.6	27.6
2	44.3	44.0
3	60.5	58.3
4	70.5	70.5
5	82.9	81.0
6	--	90.1
7	--	97.9
8	--	104.6

[1] Size of fish determined from regression of scale diameter (R) and fork length (L):

$$R = 0.0210L + 0.09$$

[2] Size of fish determined by using average size of fish with four rings (most abundant group) in the Walford (1946) regression line:

$$Y = 0.8614X + 20.3$$

where Y is size of fish at N + 1
and X is size of fish at N

ages. Although Yabuta and Yukinawa (1963) investigated changes in marginal increment of scales with time, they were unable to establish the time of annulus formation to their satisfaction. They suggested the possibility that rings are formed between August and December; however, they did not discount the possibility that ring formation takes place over an extended period or even possibly twice a year. The authors estimated the asymptotic size by the Walford method and obtained a value of 146.3 cm. They reported that this value was considerably less than the asymptotic size of 289 cm. calculated by Nose, Kawatsu, and Hiyama (1957) and larger than the estimate of 118 cm. made by Otsu (1960) on the basis of tag recoveries.

Figures 2, 3, 4, and 5 show the growth curves of albacore estimated by various investigators. Since tag recoveries strongly suggest a single stock of albacore in the North Pacific, the various curves have been separated by the method of aging.

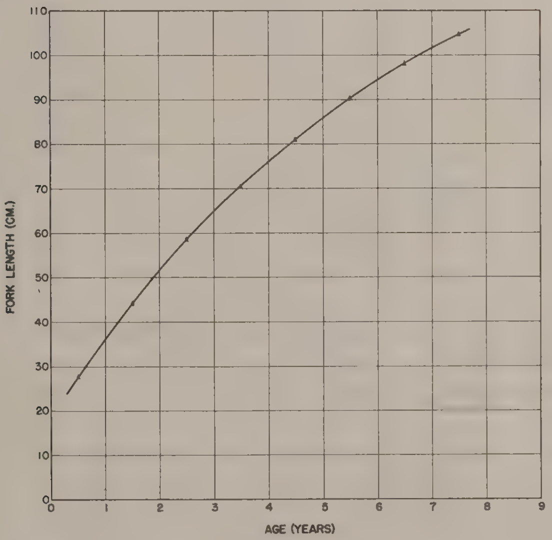

Figure 1.--Growth of albacore estimated from annuli on scales (Yabuta and Yukinawa, 1963[1]).

[1] Calculated size at time of annulus formation. Data plotted are those of method B, table 1.

Figure 2 shows four growth curves for albacore from the North Pacific. Partlo (1955) examined vertebrae from 531 albacore caught in the eastern Pacific in 1950 and established a growth rate which was slower than those determined by other investigators. Although Uno's curves (Uno, 1936a, 1936b) and the curve of Aikawa and Kato (1938) agree well, most investigators now believe that results from vertebral studies do not accurately describe the growth of albacore. One of the major criticisms

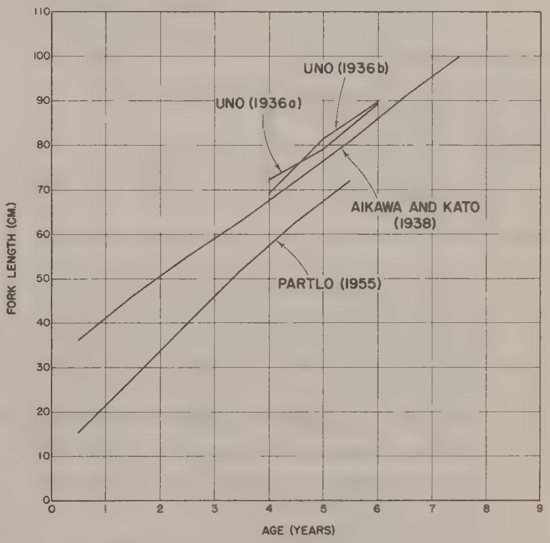

Figure 2.--Growth of albacore estimated from annuli on vertebrae (Aikawa and Kato, 1938[1]; Partlo, 1955[1]; Uno, 1936a[2]; Uno, 1936b[2]).

[1] Calculated size at time of annulus formation.

[2] Average size of fish with a given number of annuli.

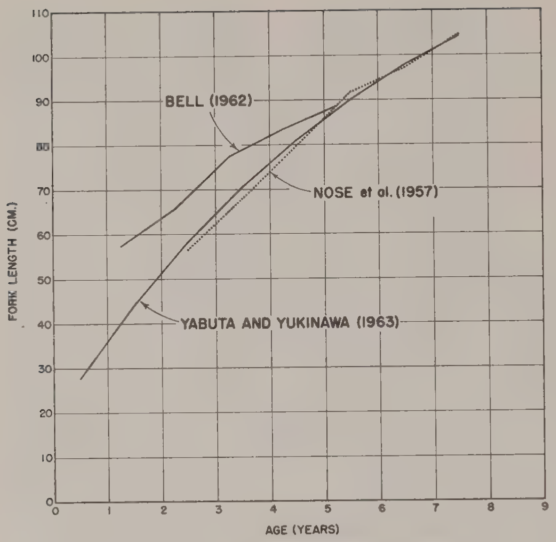

Figure 3.--Growth of albacore estimated from annuli on scales (Yabuta and Yukinawa, 1963[1/]; Bell, 1962[2/]; Nose et al., 1957[2/]).

[1/] Calculated size at time of annulus formation.

[2/] Average size of fish with a given number of annuli.

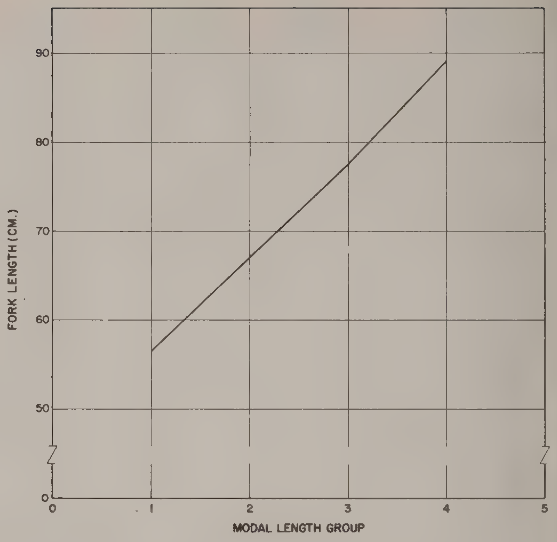

Figure 4.--Growth of albacore estimated from length-frequency distribution (Suda, 1954).

has been that over a large part of the lifespan of the albacore the size-at-age relationship is nearly a straight line. As a result the von Bertalanffy parameters could not be calculated for these early data (table 2). Furthermore, the asymptotic size of Uno's fish (105 cm.) is considerably smaller than the maximum size of albacore taken by various fisheries in the North Pacific, which is, according to Otsu (1960), 124 cm.

The results of three studies of albacore growth by the scale method are shown in figure 3. The curves of Nose et al. (1957) and Yabuta and Yukinawa (1963) agree with each other. The most interesting and surprising feature indi-

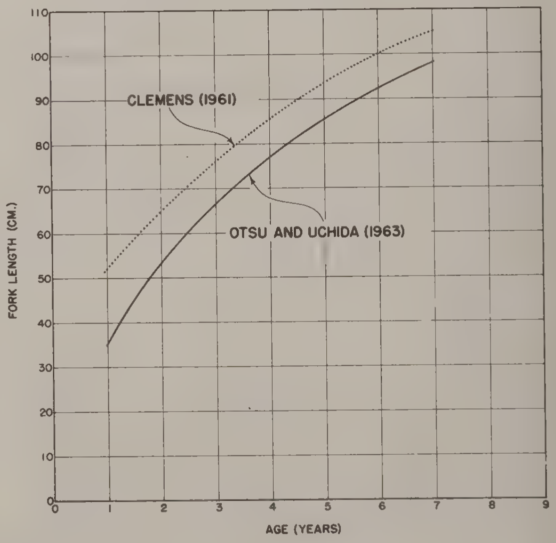

Figure 5.--Growth of albacore estimated from tag-recovery data.

cated in figure 3 is the marked difference between the growth curves derived by Bell (1962) and Yabuta and Yukinawa (1963). For fish with two and three rings, the lengths of albacore in Bell's study are about 15 and 10 cm., respectively, greater than those of Yabuta and Yukinawa. The von Bertalanffy parameters are given in table 2. The asymptotic size of 109 cm. calculated

Table 2.--Estimates of parameters of von Bertalanffy growth function for albacore

Area	Investigator(s)	Method of analysis	Parameters			Size range of fish (cm.)	Comments
			L_∞ (cm.)	K	t_o		
Western North Pacific Ocean	Uno (1936a)	Vertebrae (1935 samples)	-	-	-	72-90 (avg. of age groups)	Parameters unobtainable from data provided by author.
Do.	Uno (1936b)	Vertebrae (1936 samples)	104.8	0.431	1.504	69-90 (avg. of age groups)	Parameters computed from data provided by author.
Do.	Aikawa and Kato (1938)	Vertebrae	-	-	-	57-106	Parameters unobtainable from data provided by authors.
Eastern North Pacific Ocean	Partlo (1955)	do.	225.2	0.064	-0.060	53-83	Parameters computed from size at time of ring formation; data provided by author.
North Pacific Ocean	Nose, Kawatsu, and Hiyama (1957)	Scales (1952-53 samples)	-	-	-	65-120	Parameters unobtainable from data provided by authors; size taken at time of ring formation.
Do.	do.	do.	114.4	0.308	0.818	65-120	Parameters computed from data on mean observed length provided by authors.
Do.	do.	Scales (1953-54 samples)	324.8	0.038	-2.356	50-120	Parameters computed from data on size at time of ring formation.
Do.	do.	do.	145.3	0.159	-0.056	50-120	Parameters computed from data on mean observed length provided by authors.
Eastern North Pacific Ocean	Bell (1962)	Scales	1087.9 (mm.)	0.2247	-2.2728	51-94	Author's values.
Western North Pacific Ocean	Yabuta and Yukinawa (1963)	do.	146.3	0.150	-0.396	48-95	Parameters computed from data on size at time of ring formation provided by authors.
Do.	Suda (1954)	Size frequencies	-	-	-	57-110 (modal sizes)	Parameters unobtainable from data provided by author.
North Pacific Ocean	Otsu (1960)	Tag recoveries	118.8	0.250	1.999	60-91 (at release)	Parameters computed from data on size at age provided by author; sizes estimated from Walford transformation method.
Do.	Clemens (1961)	do.	1356 (mm?)	-0.17	1.87	54-77 (at release)	Author's values.

by Bell (1962) is considerably lower than the estimate of 146 cm. from the data provided by Yabuta and Yukinawa (1963).

Finally, it should be noted with reference to age determination of albacore by hard parts that Otsu and Uchida (1959) concluded that this method was not applicable to albacore taken in the central North Pacific. As indicated earlier the conflicting results by investigators are at variance with the existence of a single intermingling population as evidenced by tagging.

Suda (1954), who examined size-frequency distributions of albacore from the western North Pacific, suggested that the modal groups discernible in the distributions were age groups. Figure 4 shows the average size of the modal groups for the period 1948-52. Parameters of the von Bertalanffy equation were unattainable with Suda's data (table 2).

Probably the best estimate of growth for tunas is obtained from recoveries of tagged fish. More studies are needed, however, to determine the effects of tagging on the behavior and growth of fishes. The tagging method is not used extensively for tunas because of the high cost and the generally low recovery rate. Otsu (1960) and Clemens (1961) were able to estimate albacore growth from only a few recoveries--Otsu with data from 11, Clemens with data from 21. In an attempt to describe the complete growth curve, particularly that portion falling below the point of inflection, Otsu (1960) fitted the data to a Gompertz equation. Because the initial growth shown by the Gompertz curve appeared to be unreasonably slow (3 years to attain a size of 30 cm.), Otsu and Uchida (1963) postulated that the 30-35 cm. albacore which occasionally appeared in the commercial catch were 1-year-old fish. On this basis, they reduced Otsu's 1960 assigned ages by 2 years. Figure 5 shows the age and growth curves of Otsu and Uchida (1963) and Clemens (1961). Although the assigned ages do not agree, the curves are parallel and a shift of 1 year would make them agree closely.

SKIPJACK TUNA

Although landings of skipjack tuna in the Pacific are the highest among the tuna species, and have consistently exceeded 150,000 short tons (Johnson, 1959), studies of the age and growth of this species have been surprisingly few. Bell (1964) reported that up to 1962 there were only six such studies. Because a number of subpopulations of skipjack tuna appear to exist in the Pacific, I shall review the studies by area, rather than by method of age determination.

Recently Rothschild (in press) examined tag-recovery data for skipjack tuna from a study conducted in the Hawaiian Islands in 1958. He derived a growth by means of the von Bertalanffy growth function curve from 35 recoveries in which the time at liberty of the fish extended over a range of 171 to 420 days. Because of the narrow range in fish sizes and the relatively short-term recoveries, Rothschild was unable to estimate the parameters of the growth function by the methods outlined in Beverton and Holt (1957) and Gulland and Holt (1959). Assuming t_0 to equal 0, Rothschild used an iterative least square method developed by Fabens (1965) to obtain estimates of K (0.77) and L_∞ (82.3 cm.). The resulting growth curve is shown in figure 6 and the von Bertalanffy parameters are listed in table 3.

Brock (1954) estimated the size at age of skipjack tuna in Hawaiian waters by analyzing the progression of modes in length-frequency distributions. These data are compared with the results of Rothschild in figure 6. Rothschild advanced the possibility that the extremely rapid growth established by Brock may be due to the presence of fish of more than one age in the larger modal size group. A compounding element mentioned by Rothschild was the possibility of size-specific movement of skipjack from the eastern into the central Pacific waters. According to his hypothesis (Rothschild, 1965) skipjack of approximately 2 years old are not fully recruited in the central Pacific fishery. Assuming more than one age group in the larger modal size distribution in Brock's study, the reduced representation of these 2-year-old fish in the Hawaiian fishery would tend to further overestimate the growth rate.

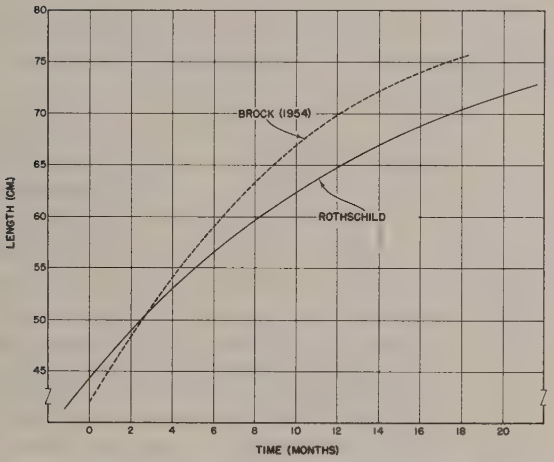

Figure 6.--Growth of skipjack tuna from Hawaiian waters estimated from length frequency and tag recoveries. (Adapted from Rothschild, in press.)

The growth of skipjack tuna in the northwestern Pacific (fig. 7) was determined by Aikawa and Kato (1938). As with their results on the other tuna species, Aikawa and Kato obtained an essentially linear curve. The linearity resulted in a questionable asymptotic size of 272.7 cm. (table 3). Kawasaki (1963) gave growth data for skipjack tuna in the western Pacific based on length frequencies. These data show some variation in growth between year classes (fig. 8) and are slightly less than growth estimates computed by Rothschild for skipjack in the central Pacific.

Table 3.--Estimates of parameters of von Bertalanffy growth function for skipjack tuna

Area	Investigator(s)	Method of analysis	Parameters			Size range of fish (cm.)	Comments
			L_∞ (cm.)	K	t_0		
Western North Pacific Ocean	Aikawa and Kato (1938)	Vertebrae	272.7	0.040	-1.582	32-78	Parameters computed from data provided by authors.
Central North Pacific Ocean	Brock (1954)	Size frequencies	85.0	1.014	0.317	40-80 (modal groups)	Parameters computed from data provided by author.
Do.	Rothschild (in press)	Tag recoveries	82.3	0.77	-	40-50 (at release)	Author's values.

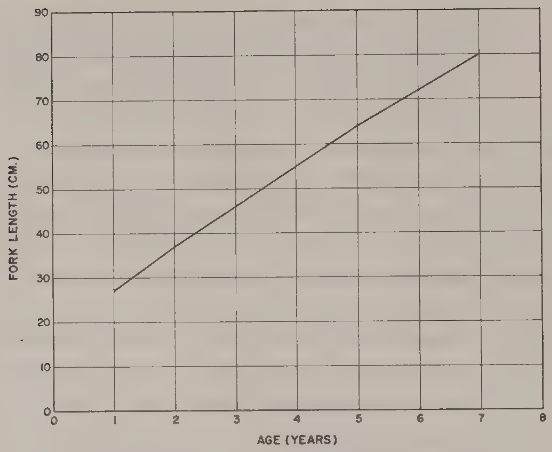

Figure 7.--Growth of skipjack tuna from the Pacific Ocean estimated from annuli on vertebrae (Aikawa and Kato, 1938[1]).

[1] Calculated size at time of annulus formation.

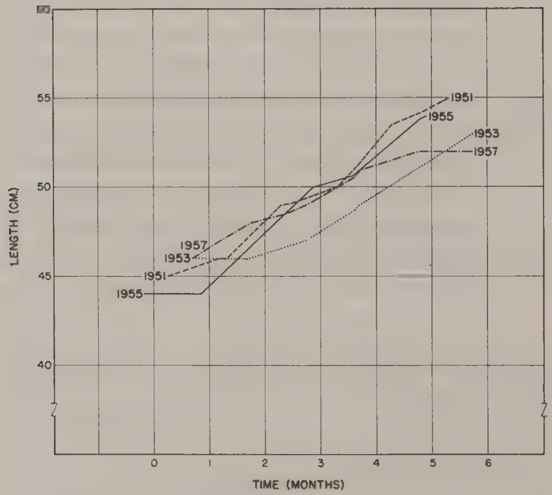

Figure 8.--Growth of skipjack tuna from the northwestern Pacific estimated from length-frequency studies. (Adapted from Rothschild (in press) based on data from Kawasaki (1963).)

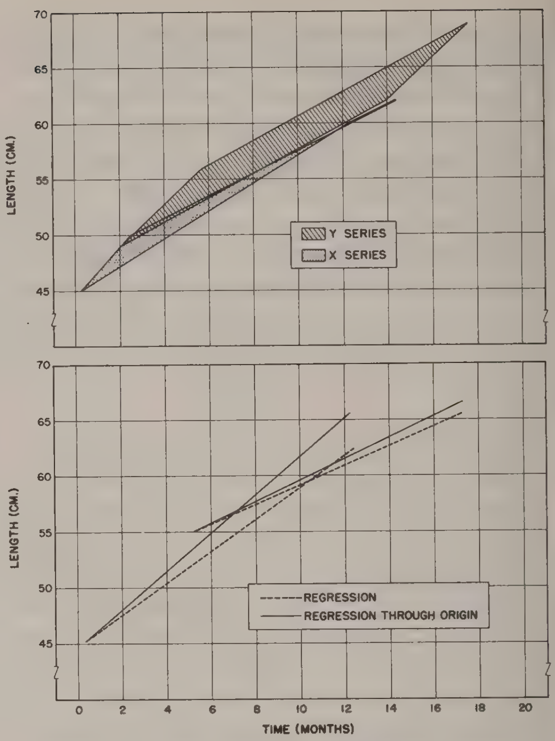

Figure 9.--Growth of skipjack tuna from the eastern Pacific. (Upper) Estimates from length-frequency data of the two groups of fish (X and Y series) entering the eastern Pacific. (Lower) Tag-recovery data. (Adapted from Rothschild (in press) based on data from Schaefer (1961) and Schaefer et al. (1961).)

In the eastern Pacific the growth of skipjack tuna as determined by modal sizes (Schaefer, 1961) agreed reasonably well with the limited tag-recovery data (Schaefer, Chatwin, and Broadhead, 1961) (fig. 9).

The curves of Kawasaki (1963), Rothschild (in press), Schaefer (1961), and Schaefer et al. (1961) agree generally.

YELLOWFIN TUNA

Several studies have been made of the age and growth of yellowfin tuna from the western Pacific. With the exception of the estimate provided by Nose et al. (1957), all of the recent studies suggest that growth in the western Pacific is very rapid during early life. Yabuta, Yukinawa, and Warashina (1960) compared their results with Nose et al. (1957), and pointed out that if the latter authors assumed the formation of two rings per year on the scales, as the former authors did, the resulting curves would agree well with those derived by other investigators.

Yabuta and Yukinawa (1957) analyzed length-frequency data of yellowfin tuna caught near Japan in 1953-55. They confined their study to the area north of lat. 20° N. and between long. 130° and 140° E. In assigning ages to the modal length groups the authors assumed that the modal group at about 51 cm. were fish in the 0 age group. The results of their studies are given in table 4 and shown in figure 10. The authors pointed out that their estimate of the growth of yellowfin tuna was comparable with that of Moore (1951) for fish taken in Hawaiian waters (fig. 10).

In a second study, Yabuta and Yukinawa (1959) examined size-frequency data of fish caught in the Equatorial Countercurrent and the South Equatorial Current. They noted some variation in growth of the different "year classes." In a comparison of equatorial yellowfin tuna with those taken farther north (Yabuta and Yukinawa, 1957), they found the growth rates to be about the same for the younger age groups. The curves tended to diverge, however, at higher ages, when the equatorial yellowfin tuna showed a slower rate of growth. Table 4 gives the growth data for yellowfin tuna from the equatorial Pacific.

In a third study, Yabuta et al. (1960) examined 2,087 scales collected in 1956-59. As in the study of albacore scales (Yabuta and Yukinawa, 1963), they considered only a relatively small

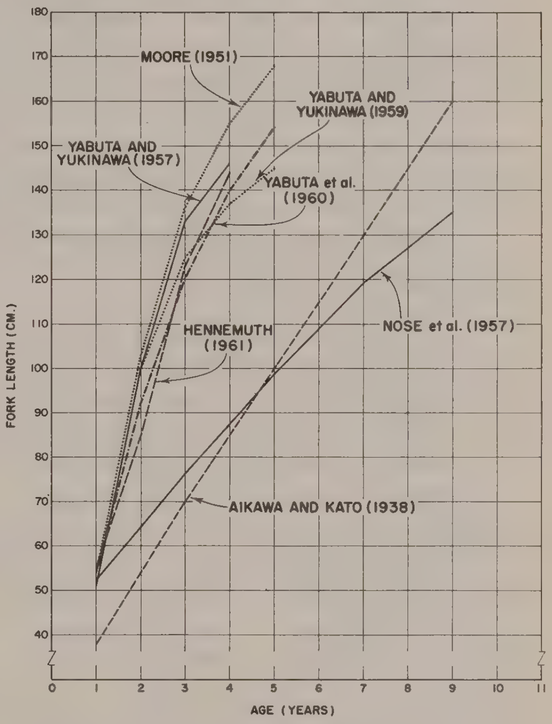

Figure 10.--Growth of yellowfin tuna from the Pacific Ocean estimated from annual rings on scales (Nose et al., 1957[1]; Yabuta et al., 1960[2]); from annual rings on vertebrae (Aikawa and Kato, 1938[2]); and from length frequencies (Hennemuth, 1961; Moore, 1951; Yabuta and Yukinawa, 1957, 1959).

[1] Average size of fish with a given number of annuli.

[2] Calculated size at time of annulus formation.

percentage (42.3) of the scales readable. The authors established the relationship between scale length in mm. (R) and fork length in cm. (L) and determined the size of fish at time of ring formation. By examining the seasonal change in size of the marginal increment of scales the authors made an important finding regarding ring formation: two rings are formed each year in yellowfin tuna--one in March-April and the other in September-October. On this evidence they pointed out (as mentioned earlier) that the estimate of growth of yellowfin tuna by Nose et al. (1957) would agree closely with their curve if this factor was taken into consideration. The size-at-age data from Yabuta et al. (1960) are given in table 4.

Figure 10 shows the growth curves of yellowfin tuna estimated by various investigators. As discussed by Yabuta et al. (1960), the curves of Nose et al. (1957), may be misrepresented by assuming annual ring formation. In general it appears that the growth of yellowfin tuna in the three major areas--eastern Pacific (Hennemuth, 1961), central Pacific (Moore, 1951), and western Pacific (Yabuta and Yukinawa, 1959; Yabuta et al., 1960)--is very rapid in early life.

The parameters of the von Bertalanffy growth equation for the various studies are listed in table 5. The only anomalous value of the estimates of asymptotic size appears to be that derived from the data of Aikawa and Kato (1938).

BIGEYE TUNA

Age and growth of bigeye tuna have been estimated recently from three different areas of the Pacific Ocean. In the western Pacific, Yukinawa and Yabuta (1963) worked with length-frequency data as well as scales to obtain estimates of growth. In the central Pacific, Shomura and Keala (1963; MS.[1]) used weight-frequency data to establish the age and growth of

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[1] Shomura, R. S., and B. A. Keala. MS. Recomputation of growth parameters of bigeye tuna (Thunnus obesus) from Hawaiian waters. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii.

Table 4.--Summary of recent growth studies of yellowfin tuna from the western Pacific

Area	Investigator(s)	Method	Length (cm.) of age group				
			0	I	II	III	IV
Japanese waters	Yabuta and Yukinawa (1957)	Size (length) frequency	<51	100	133	146	-
Western equatorial Pacific	Yabuta and Yukinawa (1959)	do.	<51	100	125	137	145[1]
Western Pacific	Yabuta, Yukinawa, and Warashina (1960)	Scales[2]	54.3	92.7	120.8	-	-
Do.	do.	Scales[3]	54.3	92.3	120.1	139.9	154.1

[1] Yabuta and Yukinawa state that this length is presumed.

[2] Assignment of age groups based on the observation of Yabuta et al., that two rings formed each year.

[3] Yabuta et al., used basic data derived from scale study and used the Walford method to estimate size at each age. L_∞ = 190.1 cm.

bigeye tuna in Hawaiian waters. Finally, in the eastern Pacific, Kume and Joseph (1966) also used length-frequency data in their study of growth.

Western Pacific Ocean

The length-frequency data used by Yukinawa and Yabuta (1963) were collected from the Tokyo and Yaizu fish markets, September 1949 to March 1956. All fish were caught by longline gear in the North Pacific fishing grounds north of lat. 25° N. In a preliminary analysis, the authors found that only the data from west of long. 180° appeared to be internally consistent. For a given time

Table 5.--Estimates of parameters of von Bertalanffy growth function for yellowfin tuna

Area	Investigator(s)	Method of analysis	Parameters			Size range of fish (cm.)	Comments
			L_∞ (cm.)	K	t_o		
Western North Pacific Ocean	Aikawa and Kato (1938)	Vertebrae	1778.5	0.009	-1.406	33-90	Parameters computed from data provided by authors.
Pacific Ocean	Nose et al. (1957)	Scales	271.3	0.060	-2.530	75-170 (estimated)	Parameters computed from combination data on size at ring formation for all areas provided by authors.
Western North Pacific Ocean	Yabuta and Yukinawa (1957)	Size frequencies	168.9	0.564	0.368	30-150	Parameters computed from data provided by authors.
Western Pacific Ocean	Yabuta and Yukinawa (1959)	do.	151.6	0.663	-0.620	77-150 (modal groups)	Do.
Pacific Ocean	Yabuta, Yukinawa, and Warashina (1960)	Scales	197.5	0.312	-1.030	61-161	Parameters computed from scale-reading data provided by authors.
Do.	do.	do.	191.1	0.327	-1.020	61-161	Parameters computed from estimated lengths derived from Walford transformation of scale data.
Central Pacific Ocean	Moore (1951)	Size frequencies	190.2	0.454	0.267	5-265 lbs.	Parameters computed from data provided by author.
Eastern Pacific Ocean	Hennemuth (1961)	Size frequencies 1953 year class	172	0.047	10 mo.	50-146 (modal groups)	Author's values.
Do.	do.	Size frequencies 1954 year class	162	0.055	8 mo.	do.	Do.
Do.	do.	Size frequencies 1955 year class	173	0.055	11 mo.	do.	Do.
Do.	do.	Size frequencies avg. 1953-55 year classes	169	0.05	10 mo.	do.	Do.

period the length-frequency distribution from areas to the east of long. 180° had modal sizes which were progressively larger from west to east. Therefore Yukinawa and Yabuta (1963) confined their analysis to the age and growth of bigeye tuna west of long. 180°. They examined the progression of modal sizes and established a size-on-age relationship of bigeye tuna for the month of April (table 6).

Table 6.--Average modal size for April of bigeye tuna from the North Pacific (adapted from Yukinawa and Yabuta, 1963)

Approximate age (years)	1	2	3	4	5
Fork length (cm.)	-	72	100	121	142

In addition to the size-frequency study, Yukinawa and Yabuta (1963) also examined scales from 1,622 bigeye tuna landed at the Tokyo and Yaizu fish markets from 1957 to 1961. The fish were taken by longline and pole-and-line gear in North Pacific north of lat. 10° S. Of the 1,622 scale samples examined, only 463 (28.5 percent) were considered readable. The same investigators reported scale readability of 34.7 percent for albacore (Yabuta and Yukinawa, 1963). Scales from small (young) fish were considerably easier to read than scales from larger (older) fish. The scales from bigeye tuna larger than 130 cm. were unreadable.

Yukinawa and Yabuta (1963) determined the relationship between scale diameter and fork length and established the size at time of ring formation for fish with ring counts of one to six. On the basis of changes in size of the marginal increment of scales with time, the authors concluded that two rings were formed each year--one in April and the other in September-October. From data

Table 7.--Size (cm.) at time of ring formation for bigeye tuna (adapted from Yukinawa and Yabuta, 1963)

Assumed age	Number of rings	Calculated from scale measurements	Walford method	von Bertalanffy method
	-		21	21
1	1	44	40	40
	2	61	57	58
2	3	77	73	73
	4	89	87	87
3	5	102	100	100
	6	116	111	111
4	-	-	121	122
	-	-	130	131
5	-	-	139	139
	-	-	146	147

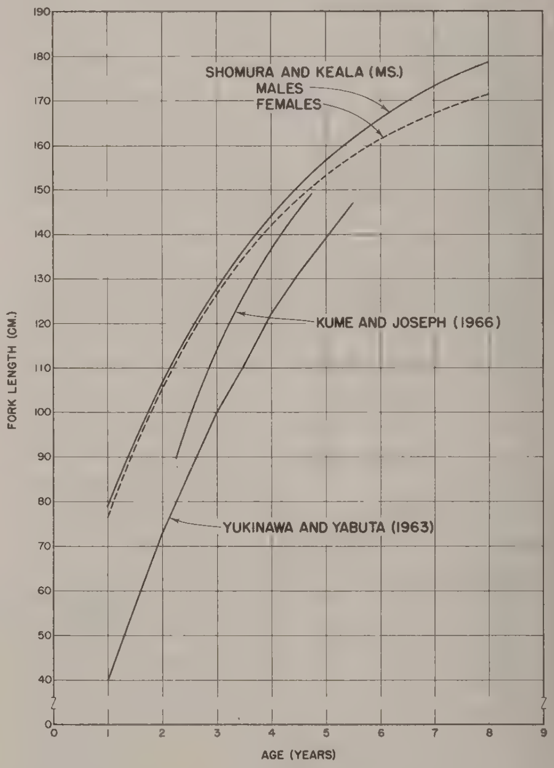

Figure 11.--Growth of bigeye tuna from the Pacific Ocean estimated by the size-frequency method (Kume and Joseph, 1966; Shomura and Keala, MS.), and from rings on scales (Yukinawa and Yabuta, 1963).

provided by the scale analysis the authors made a second estimate of the size at ring formation by using the Walford transformation. Furthermore, with the asymptotic size from the Walford method, Yukinawa and Yabuta (1963) also calculated a third estimate of size-at-age by fitting the von Bertalanffy equation to the data obtained from the Walford method (table 7 and fig. 11).

Central Pacific Ocean

Shomura and Keala (1963) analyzed weight-frequency data of bigeye tuna caught with longline gear in Hawaiian waters. They used data collected from April 1960 through March 1961 and, with some basic assumptions, constructed a composite growth curve. Since publication of their paper, the authors have uncovered an error in the procedure used. In a more recent paper, they discounted their earlier results on the basis that weight data could not properly be used with the Walford method to obtain an estimate of the asymptotic size. The authors have recomputed the estimates of the von Bertalanffy parameters by means of length data converted from the original weight data. The results of Shomura and Keala (MS. see footnote 1) are given in table 8 and the curves for male and female bigeye tuna are shown in figure 11. Males were found to grow faster than females and the asymptotic size of male bigeye tuna of 196.7 cm. closely approximated the largest male bigeye tuna on record (198 cm.) at Biological Laboratory in Honolulu.

Table 8.--Estimated size-at-age of bigeye tuna from Hawaiian waters (Shomura and Keala, MS.)

Assumed age	Fork length (cm.)	
	Male	Female
1	79.1	76.7
2	106.8	105.4
3	127.9	126.5
4	144.0	141.8
5	156.4	153.0
6	165.8	161.0
7	173.1	167.1
8	178.6	171.3

Eastern Pacific Ocean

In 1956 the Japanese longline fleet began fishing in the eastern Pacific (Suda and Schaefer, 1965). Before the expansion of the Japanese fishery into these waters, tuna fishing was restricted to surface methods (purse seine and pole and line) and captures of bigeye tuna were only incidental to the taking of yellowfin and skipjack tunas. The subsurface-fishing longline gear uncovered a large resource of bigeye tuna in the eastern Pacific.

Kume and Joseph (1966) studied the progression of modal length groups of bigeye tuna, to obtain estimates of the age and growth. The data were collected from 1958 to 1964 and were summarized by quarter years. The authors were able to trace part of the growth history of 7-year classes; however, at any single time only 3-year classes were discernible in the sample. The

Table 9.--Growth of eastern Pacific bigeye tuna (adapted from Kume and Joseph, 1966)

Age in months	Average size (fork length, cm.)	von Bertalanffy method (fork length, cm.)
27	92.0	89.7
30	97.0	98.5
33	103.3	106.6
36	113.0	113.8
39	122.0	120.6
42	129.4	126.6
45	131.5	132.0
48	136.0	137.0
51	143.3	141.5
54	144.3	145.6
57	147.5	149.4

Table 10.--Estimates of parameters of von Bertalanffy growth function for bigeye tuna

			Parameters				
Area	Investigator(s)	Method of analysis	L_∞ (cm.)	K	t_o	Size range of fish (cm.)	Comments
Western North Pacific Ocean (north of lat. 25° N. and west of 180°)	Yukinawa and Yabuta (1963)	Size frequency	257.5	0.156	-0.107	Modal sizes estimated to be 65-150	Parameters computed from data provided by authors.
Pacific Ocean (north of lat. 10° S.)	do.	Scales	215	0.10412	0.0010995	Estimate 51-160	Authors' values; time (t) in half-year units.
Do.	do.	Scales (same basic data as above)	213.1	0.212	0.017		Parameters computed by graphic method from data provided by authors.
Central Pacific Ocean (Hawaiian Islands)	Shomura and Keala (MS.)	Size frequency (males)	196.7	0.267	-0.929		Authors' values.
Do.	do.	Size frequency (females)	183.0	0.316	0.718		Do.
Eastern Pacific Ocean (east of long. 130° W. and between lat. 10° N. and 25° S.)	Kume and Joseph (1966)	Size frequency	186.95	0.095	2.11	39-209	Authors' values; time (t) in quarter-year units.
Pacific-wide, north of lat. 10° S.	Nose et al. (1957)[1]	Scales	195.2	0.106	-1.128	Mean observed length for 58-109	Parameters based on mean observed length by age provided by authors.

[1] Parameters could not be obtained for data on size at ring formation provided by authors.

rates of growth of the various year classes closely approximated each other. Using the age estimates of other investigators and assuming a spawning peak in the second quarter of the year, Kume and Joseph (1966) developed a size-at-age relationship by fitting the von Bertalanffy growth equation to the data (table 9 and fig. 11).

Kume and Joseph (1966) compared their results with those of Shomura and Keala (1963) from the central Pacific and of Yukinawa and Yabuta (1963) from the western Pacific. They noted that their curve fell between the growth curves for the central Pacific bigeye tuna and the western Pacific bigeye tuna. They pointed out that these differences may be real, but that the possibility of errors in the assignment of ages should not be entirely discounted. In general, the three curves of growth of bigeye tuna from the three different areas in the Pacific were reasonably close to one another (table 10).

ACKNOWLEDGMENTS

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ESTIMATES OF YIELD FOR PACIFIC SKIPJACK AND BIGEYE TUNAS

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ABSTRACT

Potential yields of skipjack tuna (Katsuwonus pelamis) and bigeye tuna (Thunnus obesus) in the central Pacific were estimated by a population-simulation method. The estimate indicates a maximum yield of 225,000 metric tons of skipjack tuna per year, requiring double the effort expended during 1952-61. The present yield of the skipjack tuna fishery in the eastern Pacific is 68,000 metric tons per year. The estimated average sustainable yield for the bigeye tuna is 78,000 metric tons; that figure is already exceeded by the catch of the Japanese longline fleet.

INTRODUCTION

The estimates reported below were derived by the population-simulation method described by Silliman (in press). Essentially this method consists of constructing the course of population and yield, by using observed or assumed values of natural and fishing mortality plus observed or assumed growth and recruitment curves. Resulting calculated catches are then compared with actual catches to test the agreement with the model. If agreement between actual and calculated catches is poor, one or more of the parameters is changed, and successive trials are made until reasonable agreement between calculated and actual yields is attained or found unattainable.

This method was applied to data for the eastern Pacific skipjack tuna fishery and the Japanese Pacific longline fishery for bigeye tuna. The resulting estimates are considered to be rough preliminary approximations. Symbols used, adapted from or added to international notation (Holt, 1960), are as follows:

t and t_r = age in years, total and at recruitment to fishable stock;

P_t = weight of all fish of a given year class surviving at age t;

$\hat{Y}_w$ = estimated yield in weight, per year;

i = subscript referring to individual year classes;

R_w = initial weight of recruits to fishable stock for a single year class;

n = number of year classes in the fishable stock;

$\bar{l}$ = average length at capture;

l_c = length at recruitment;

K and L_∞ = constants of von Bertalanffy growth curve;

P_c = ratio of density of mature stock to density which gives maximum recruitment;

F, M, and Z = instantaneous rates of fishing, natural, and total mortality, respectively;

f = fishing effort in standard units;

q = catchability coefficient = F/f;

W_t = weight of individual fish at time t;

W_r = weight of individual fish at recruitment;

G, g = constants of Gompertz curve.

In addition to these parameters, an assumed stock-recruitment relation

$$(R_w = P_c \exp 1 - P_c)$$

and a Gompertz growth-in-weight curve

$$(W_t = W_r \exp G - G \exp - g\ (t - t_r))$$

were used in simulation. Only F, M, and the stock-recruitment relation were varied in the trial and approach error.

SKIPJACK TUNA

Data from the eastern Pacific bait boat and purse seine fishery were used, because that fishery takes the majority of the U.S. Pacific catch of skipjack tuna. Values for the models were obtained as follows:

1) Annual catch (table 1). Data for the period 1944-61 were derived from Waldron (1963) and Alverson (1963).

2) Fishing effort (table 1). Values were scaled from figure 4 in Bureau of Commercial Fisheries (1963).

3) Mortality rates. Total mortality Z = 0.8 was calculated by B. J. Rothschild (personal communication) according to the formula:

$$Z = \frac{K\ L\infty^{-\bar{l}}}{\bar{l} - l_c}$$

It was assumed to apply to the recent period of increased yield, 1952-61.

Recruitment was assumed to occur at an age of 1 year. This assumption is based on length frequencies from the eastern Pacific fishery published by

Table 1.--Catch and fishing effort, eastern Pacific bait boat and purse seine fishery for skipjack tuna, 1944-61

Year	Catch, 1,000 metric tons[1]	Effort, 1,000 boat-days[2]
1944	14	7
1945	15	9
1946	19	16
1947	24	19
1948	28	22
1949	37	22
1950	59	25
1951	55	25
1952	41	34
1953	61	38
1954	79	29
1955	58	25
1956	68	30
1957	58	36
1958	75	38
1959	81	34
1960	55	33
1961	72	36
Total	899	478

[1] 1944-59 from Waldron (1963), 1960-61 from Alverson (1963). By error the catches for 1960 and 1961 are in short rather than metric tons. Correction to metric tons would not substantially alter the conclusions of this report.

[2] Scaled from Bureau of Commercial Fisheries (1963), figure 4.

Broadhead and Barrett (1964), indicating entry at a length of 40 cm., corresponding to an age of 12 months on the growth curve of Rothschild (in press). Furthermore, it was assumed that skipjack tuna are taken by the eastern Pacific fishery only during ages 1 and 2. Again, frequencies of Broadhead and Barrett show the great majority of fish at lengths less than 70 cm., corresponding to age 36 months on Rothschild's curve. These assumptions are consistent with the general hypothesis of Rothschild (1965) that most eastern Pacific skipjack tuna originate in the central Pacific, remain only briefly in the eastern Pacific, and then move offshore toward the central Pacific to spawn.

Following the above reasoning, fishing mortality (F) was assumed to apply only to ages 1 and 2, and natural mortality (M) alone at ages 3 and above.

Trials employed assumed values of M from M = 0.2 to M = 0.7. The value of q in F = qf was determined from the relation between mean effort $\bar{f}$ and the assumed $\bar{F} = Z - M$ for the 1952-61 period. F for each year was then calculated by using yearly values of f (table 1), as indicated above.

4) Growth curves. Growth in weight was estimated from the curve of growth in length developed by Rothschild (in press). He fitted a von Bertalanffy curve to data derived from growth of tagged fish. By use of a length-weight relation (Nakamura and Uchiyama, 1966), points from the Rothschild curve were converted to weights-at-age. These in turn were fitted with a Gompertz curve as described by Silliman (in press).

5) Recruitment curves. An assumed recruitment curve was adopted for the first trial, and modified for subsequent trials. The curve employed in the yield estimates (fig. 1) is similar in general form to the Ricker (1954) curve $R_W = P_c \exp 1 - P_c$. It was chosen to pass through two points: 1) the origin, and 2) a point based on the assumption that recruitment and growth exactly balanced catch and mortality at the beginning (1944) of the trial. The shape of the curve was based on general experience with other fisheries, such as those for the California sardine (Radovich, 1962) and the New England haddock (Ricker, 1954). The commercial stock used on the axis of abscissas comprises all fish at or over the recruitment age of 1 year ("knife edge" selection).

Six trials were made by using the values listed above, and using M = 0.2 to 0.7. $Z = \bar{F} + M$ was kept constant at 0.8 for the period 1952-61. For each trial the sum of squared deviations of calculated from actual catches was computed as listed below:

M	Σd^2	M	Σd^2
0.2	2413	0.5	2850
0.3	2338	0.6	3286
0.4	2431	0.7	2855

Although the trials do not provide strong contrasts as a basis of selection, those bracketing M = 0.3 change in a regular

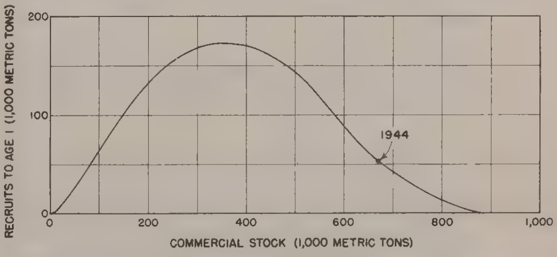

Figure 1.--Assumed stock-recruitment relation of skipjack tuna used in trial with M = 0.3, $\bar{F}$ for 1952-61 = 0.5.

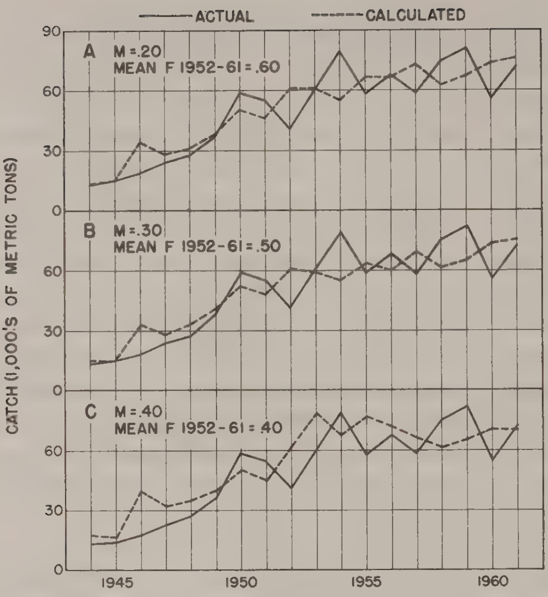

Figure 2.--Comparison of actual and calculated catches, eastern Pacific skipjack tuna.

manner. Since this trial gave the smallest sum of squared deviations, the value M = 0.3 was adopted for yield estimation. This simulation included also parameters R_w (from curve, fig. 1), $G = 2.85$, $g = 0.695$, $t_r = 1.0$, and $F = 0.50$ in the expressions (Silliman, in press):

$$P_t = R_w \exp\left[G - G \exp -g\,(t - t_r)\right] - (F + M)\,(t - t_r)$$

and

$$\hat{Y}_w = F/Z\left[1 - \exp -Z\right] \sum_{i=0}^{i=n} P_{ti}$$

Calculated catches from M = 0.2, 0.3, and 0.4 are compared with actual catches in figure 2. Application of the selected value of M plus the other parameters as used with it, gave estimates of equilibrium yield. These were made on the assumption that the fishery would be expanded to take the larger fish now unexploited. F was therefore applied to all postrecruitment ages, instead of only ages 1 and 2 as above. Yield estimates appear in table 2.

These estimates indicate a maximum yield of 225,000 tons at F = 1.0, requiring double the effort in effect during 1952-61. If we may assume that the eastern Pacific fishery draws on stock spawned in the central Pacific (Rothschild, 1965), the rather large estimated yields may be within reason. The higher estimated yields are rather heavily dependent on the assumed recruitment curve. Also, it is possible that the broader geographic distribution of fishing effort contemplated for higher values of F may change the value of q.

Table 2.--Calculated sustainable yields, skipjack, selected values of F

F	Average sustainable yield 1,000 metric tons	Effort 1,000 boat-days from $f = \frac{F}{q}$[1]	Tons/boat-day
0.5	180	33	5.5
0.6	200	40	5.0
0.8	220	53	4.2
0.9	220	60	3.7
1.0	225	67	3.4
1.1	215	73	2.9

[1] $q = 0.01501$ from $\bar{F} = 0.5$ and $f = 33.3$, for 1952-61.

BIGEYE TUNA

Data for this species were from the Japanese longline fishery, which takes the major portion of the Pacific catch. The following parameters were used:

1) Annual catch (table 3). Data for 1953-63 are from Otsu and Sumida (1966). Subsequent to the calculations of this report, Otsu and Sumida revised their data. Changes were small, how-

ever (mean change regardless of sign was 4 percent), and substitution of the new for the old data would not alter my conclusions.

2) Fishing effort (table 3). Values for 1953-61 are from unpublished data and those for 1962-63 are from Japan Fisheries Agency, Research Division (1965 and 1966).

3) Mortality rates. Total mortality $Z = 0.4$ and natural mortality $M = 0.2$ (based on yield-per-recruit curves) were suggested by B. J. Rothschild (personal communication). These values also yield $F = Z - M = 0.2$, which was taken as the mean for the period 1953-63. Individual annual values were obtained by applying $F = qf$ to the yearly values of fishing effort, f. The constant q was obtained from the relation between mean f and mean F.

4) Growth curve. A curve of length-at-age was obtained from Kume and Joseph (1966), and was converted to weight-at-age by the length-weight relation of Rothschild (personal communication). A Gompertz curve was fitted.

5) Recruitment curves. Recruitment was assumed to occur at rounded age 3, since the size at recruitment (100 cm.) indicated by B. J. Rothschild (personal communication) lies at age 2.6 on the growth curve. An assumed recruitment curve (fig. 3) was adopted for the first trial, and modified for the second and third trials. The curve was chosen as described above for the skipjack tuna, using 1953 as the beginning of the trial.

Three trials were made by using $M = 0.20$, 0.15, and 0.10, and keeping $M + \bar{F} = 0.40$ (No. 3 above). Other constants were $G = 1.474$, $g = 0.468$, $t_r = 3.0$. Actual and calculated catches are compared in figure 4. The best fit is indicated for $M = 0.10$. Application of this value, and the other parameters used in the third trial, gave the equilibrium yields in table 4.

These results indicate a maximum yield at around $F = 0.60$, requiring twice the 1953-63 average effort.

Table 3.--Catch and fishing effort, Japanese longline fishery for bigeye tuna, 1953-63

Year	Catch, 1,000 metric tons[1]	All species effort, 100,000 hooks[2]
1953	25	566
1954	23	1,281
1955	36	1,602
1956	40	1,310
1957	41	1,560
1958	54	1,947
1959	56	2,106
1960	54	2,462
1961	79	2,640
1962	91	2,890
1963	98	3,374
Total	597	21,738

[1] From Otsu and Sumida (1966), table 1.

[2] 1953-61, unpublished data; 1962, 1963 from Japan, Fisheries Agency, Research Division (1965 and 1966). The value of F was estimated on the assumption that fishing effort for bigeye tuna changed in the same manner as total longline effort in the Pacific Ocean.

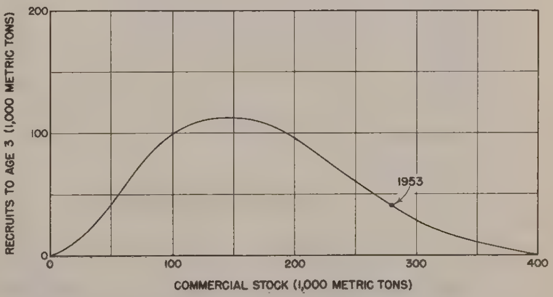

Figure 3.--Assumed stock-recruitment relation of bigeye tuna used in trial with $M = 0.1$, $\bar{F}$ for 1953-63 $= 0.3$.

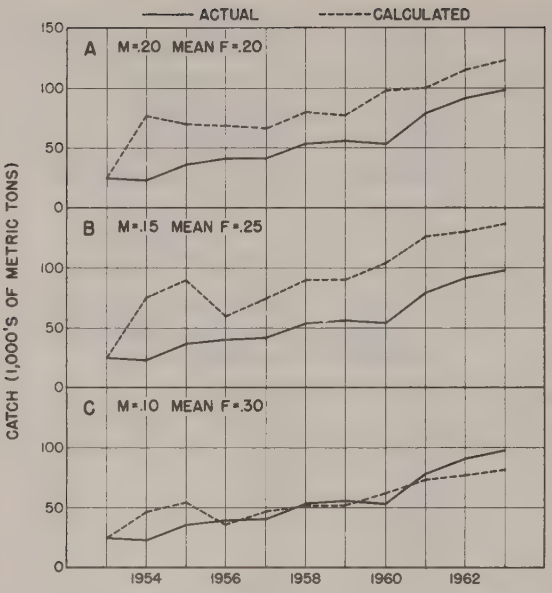

Figure 4.--Comparison of actual and calculated catches, Pacific bigeye tuna caught in Japanese longline fishery.

Table 4.--Calculated sustainable yields, bigeye, selected values of F

F	Average sustainable yield 1,000 metric tons	Effort, millions of hooks $f = \frac{F}{q}$[1]	Tons per million hooks
0.40	70	264	266
0.50	75	329	228
0.60	78	395	197
0.70	78	461	169
0.80	77	527	146
0.90	70	593	118

[1] $q = 0.001518$ from $\bar{F} = 0.30$ and $\bar{f} = 197.62$ for 1953-63.

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PLAN FOR AN ASSESSMENT OF ABUNDANCE AND YIELD OF PACIFIC TUNAS

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ABSTRACT

The catch of skipjack tuna (Katsuwonus pelamis), which dominates the Hawaiian fisheries, was 9 million pounds (4,900 metric tons) in 1964. Bigeye tuna (Thunnus obesus) ranked second with 836,000 pounds (470 metric tons), yellowfin tuna (T. albacares) third with 293,000 pounds (161 metric tons), and albacore (T. alalunga) fourth with 9,000 pounds (4 metric tons). Skipjack tuna are caught by pole and line; the other tunas are caught by longline. If a major U.S. fishery is to be developed in the central Pacific, new types of gear should be considered and the economic feasibility of expansion explored. Since accurate forecasts of yield are desirable, certain types of data on the fishes and their environment will be required. Equally necessary are conceptual models of the interaction of the various factors on each other. Such models are now being considered.

HISTORICAL BACKGROUND

The Fisheries

Since the proposed assessment is concerned with development of resources in the ocean areas surrounding Hawaii, it is pertinent first to review the history of the Hawaiian fisheries. Then brief mention will be made of the eastern Pacific and Japanese fisheries. This study is not intended to be exhaustive, and literature citations are not given. Readers interested in source materials are referred to the extensive bibliography included in the Proceedings of the World Scientific Meeting on the Biology of Tunas and Related Species (FAO Fish. Rep., No. 6, vol. 4, pp. 1853-2272, 1964). The species of tuna referred to herein are: yellowfin (Thunnus albacares); skipjack (Katsuwonus pelamis); bigeye (Thunnus obesus); albacore (Thunnus alalunga); and bluefin (Thunnus thynnus).

HAWAIIAN FISHERIES

Fishing was a primary source of food in ancient Hawaii, and many customs developed around it. At some time between the coming of Europeans to the islands and the first fish survey in 1900, commercial fisheries of considerable substance were developed. The total catch in 1900--over 6 million pounds--probably included some tunas. By 1928, 2 million pounds of yellowfin tuna and 4 million pounds of skipjack tuna were being landed annually. A reduction in catch occurred during World War II, followed by a recovery from 1945 to 1948, and catches in the range 8-17 million pounds since then.

The landings are nearly all from two fisheries: the pole and line for skipjack tuna, and the longline for albacore, yellowfin, and bigeye tunas. Fishing vessels in both fisheries are the Japanese ''sampan'' type, from 40 to 80 feet long.

Pole-and-line boats carry a crew of 6 to 14 men and fish mostly with a locally available anchovy (Stolephorus purpureus) for live bait. When a school of skipjack tuna is sighted, sprays of water and live bait are used to attract or ''chum'' the fish to the boat. Fishing is done with poles, lines, and barbless hooks. A substantial part is carried out within 90 miles of port, and the vessels usually return to port at night to unload their catches. This fishing method has changed little during the period of record, starting in the 1920's.

The Hawaiian longline boats are smaller than the pole-and-line boats, and carry smaller crews (two to five men). Longline gear consists of 140- to 200-fathom mainline sections (''baskets''), each carrying five or six hooks. Hooks are baited with frozen sardines, herring, or sauries, and 20 to 35 units are set per day. The ''string'' of gear in the water is about 5 miles long and has about 150 hooks. Catches average about three fish per 100 hooks. Before World War II the yellowfin tuna was the principal species caught, but there was a postwar shift to a predominance of bigeye tuna. Some albacore are also caught in the longline fishery.

Table 1.--Tuna catch by species, Hawaii--1945-64 (thousands of pounds)

Year	Albacore[1]	Bigeye[1]	Skipjack[2]	Yellowfin[1]	Total
1945	10	12	3,907	456	4,385
1946	43	126	5,630	1,343	7,142
1947	115	340	5,592	1,314	7,361
1948	94	640	8,384	1,006	10,124
1949	70	1,086	9,895	817	11,868
1950	60	1,842	9,511	605	12,018
1951	55	2,031	12,926	661	15,673
1952	101	2,193	7,292	719	10,305
1953	49	2,794	12,059	459	15,361
1954	28	2,751	14,021	436	17,236
1955	15	2,145	9,694	353	12,207
1956	13	2,269	11,132	211	13,625
1957	9	1,626	6,130	223	7,988
1958	16	1,593	6,834	254	8,697
1959	11	1,316	12,413	389	14,129
1960	9	1,280	7,360	302	8,951
1961	14	1,033	10,894	336	12,277
1962	17	1,208	9,415	243	10,883
1963	15	935	8,099	259	9,308
1964	9	836	9,024	293	10,162

[1] Data for 1945-52 are from Otsu, 1954, Com. Fish. Rev. 16(9): 1-17. Data for 1953-64 are from Catch Records of the Hawaii Division of Fish and Game.

[2] Data for 1945-53 are from Yamashita, 1958, U.S. Fish Wildl. Serv., Fish. Bull. 58: 253-278. Data for 1954-64 are from Catch Records of the Hawaii Division of Fish and Game.

EASTERN PACIFIC FISHERIES

The fisheries in the eastern Pacific were initially conducted almost entirely by the U.S. fleet operating out of southern California ports. After World War II the range of operations was extended, and today waters off South America provide much of the catch.

In the years before World War II the distinctive ''clipper'' type of vessel was developed for tuna fishing. These large vessels were 100 feet or more long, had live-bait tanks on deck, and had a low stern with racks from which the pole-and-line fishing was done. The manner of fishing was similar to that of the Hawaiian pole-and-line fishing described above. When large fish were being caught, two or three men attached their poles to a single line. Catches

Table 2.--Tuna catch of U.S. fleet by species, Pacific coast--1911-63
(thousands of pounds)

Year	Albacore	Bluefin	Skipjack	Yellowfin	Total
1911	850[1]				850[1]
1912	3,400[1]				3,400[1]
1913	6,600[1]				6,600[1]
1914	18,470[1]				18,470[1]
1915	21,074				21,074
1916	22,899	20,540[2]	[2]	[2]	43,439
1917	30,556	1,150	420		32,126
1918	7,265	6,240	3,024		16,529
1919	13,631	14,991	6,897	348	35,867
1920	18,877	10,530	7,957	1,965	39,329
1921	15,277	2,032	1,139	1,238	19,686
1922	13,232	2,838	11,862	7,337	35,269
1923	12,515	3,301	11,463	10,837	38,116
1924	17,695	3,241	3,781	3,063	27,780
1925	22,207	3,804	14,235	13,238	53,484
1926	2,469	6,527	20,995	12,565	42,556
1927	4,579	4,898	33,807	25,934	69,218
1928	283	13,701	15,815	32,251	62,050
1929	269	7,527	26,998	37,399	72,193
1930	286	21,921	20,486	56,654	99,347
1931	37	3,534	16,507	36,580	56,658
1932	620	1,071	21,637	36,923	60,251
1933	2	560	16,687	51,076	68,325
1934	121	18,358	14,830	60,913	94,222
1935	2,448	25,173	17,197	72,252	117,070
1936	984	18,925	26,992	78,353	125,254
1937	3,520	12,694	47,104	91,523	154,841
1938	17,726	17,728	22,654	78,318	136,426
1939	18,922	11,836	30,121	110,418	171,297
1940	14,502	19,970	56,650	113,760	204,882
1941	11,932	9,519	25,586	76,702	123,739
1942	23,540	12,845	38,735	41,467	116,587
1943	37,518	10,178	28,894	49,262	125,852
1944	52,795	20,344	30,037	63,144	166,320
1945	39,483	20,594	33,348	87,448	180,873
1946	24,142	22,032	41,088	127,247	214,509
1947	26,844	20,838	52,749	153,510	253,941
1948	49,493[3]	6,529	60,554	199,427	316,003
1949	54,794[4]	4,389	80,512	190,544	330,239
1950	72,453	2,762	126,786	187,890	389,891
1951	34,491	3,862	116,599	161,481	316,433
1952	52,558	4,577	84,844	178,819	320,798
1953	34,700	9,773	122,978	133,340	300,791
1954	26,998	21,025	153,756	119,402	321,181
1955	29,738	13,609	102,807	123,208	269,362
1956	41,338	12,626	123,717	150,923	328,604
1957	46,659	20,315	90,821	137,240	295,035
1958	38,445	30,719	123,372	123,727	316,263
1959	46,284	15,194	98,482	108,370	268,330
1960	40,202	11,952	46,304	189,307	287,765
1961	32,830	20,883	65,403	191,854	310,970
1962	45,938	31,200	92,721	124,021	293,880
1963[5]	60,685	39,065	100,601	110,141	310,492

Data for 1911-57 are from Fishery Statistics of the U.S. 1957, Statistical Digest No. 44, p. 383. Data for 1958-62 are from Fishery Statistics of the U.S. 1958-62, Statistical Digest Nos. 49, 51, 53, 54, and 56. Data for 1963 are from Fisheries of the U.S. 1963.

[1] Estimated on the basis of pack as reported by tuna canners.

[2] The catch of skipjack and yellowfin tunas has been included with that of bluefin tuna.

[3] Includes 132,000 pounds landed in Alaska.

[4] Includes 39,000 pounds landed in Alaska.

[5] Data for 1963 are preliminary.

(table 2) consisted principally of yellowfin and skipjack tunas, and were made in waters off California, Mexico, and Central America.

The west coast tuna fishery underwent a major change in the late 1950's and early 1960's. Development of nylon and other synthetic netting and use of the ''power block'' for net lifting made possible large-scale seining for tunas. The clippers rapidly converted to this method, and new large vessels entered the fishery. By the early 1960's most of the vessels were seiners. The shift in gear is reflected in comparative fleet compositions: 1958--bait boats 158, seiners 44; 1964--bait boats 35, seiners 111. Because the seines could be operated more effectively and with fewer men than the poles and lines, the U.S. fleet was better able to maintain its competitive position with the expanding low-labor-cost Japanese fisheries.

The postwar history of the eastern Pacific tuna fisheries included changes in the proportion of the catch taken by the United States and Peru. In the 5 years from 1958 to 1963, the U.S. catch declined while that of Peru increased. Subsequently the U.S. catch again increased, and the trend was thus reversed.

JAPANESE LONGLINE FISHERY

Undoubtedly, the most dramatic recent development in tropical tuna fishing of the Pacific was the meteoric expansion of the Japanese longline fishery.[1] From 1952 to 1963, the Japanese world catch increased from 146 million to 753 million pounds (table 3), about 60 percent of which was taken in the Pacific. At least part of this expansion was achieved by fishing waters progressively farther east, as shown by charts of percentage effort compiled at the Biological Laboratory, Honolulu, and also in information published by Suda and Schaefer of the Inter-American Tropical Tuna Commission. By 1962 some boats were going as far east as waters off North, Central, and South America.

The Japanese high-seas fishery is conducted with large, modern vessels, ranging to over 1,000 tons. Fishing is done in much the same manner as described above for the Hawaiian longline fishery, but on a vastly larger scale. Japanese boats set about 400 baskets of gear daily, with five hooks per basket. Thus they have 2,000 hooks spread out in a line 50 to 75 miles long. Catches in the Pacific range from zero to about 50 fish per 100 hooks per day, and consist principally of yellowfin tuna, bigeye tuna, albacore, and bluefin tuna (plus some marlins, swordfish, and sharks).

In summary, the tropical Pacific tuna fisheries have been characterized by an initial period of rapid growth from the early to mid-20th century (partly interrupted during the great depression and World War II) and an explosive expansion in the 1950's and 1960's. During the early period the three fisheries were completely separated: the Japanese in the western Pacific, the Hawaiian in the central Pacific, and the United States-Latin American (mostly United States) in the eastern Pacific. In the 1950's and 1960's the Japanese longline fishery expanded so far east that no important tropical Pacific area remained unfished. Major trends of the three fisheries are revealed in a summary of the catches (table 4).

Fishery Research [2]

As the fisheries grew, the research of national, state, and international agencies tended to grow with them. Investigations have included taxonomic and fishery surveys, life history studies, analysis of catch-effort data, population dynamics studies, studies of the effect of oceanographic conditions on distribution and abundance of tuna, and such detailed studies as behavior and physiology of tuna. Research is reviewed briefly in the same order as the fisheries described above.

In Hawaii, the tunas were included in a comprehensive taxonomic survey by Jordan and Evermann in 1901-03. Studies of fishery methods and equipment and compilations of catch statistics were included in John N. Cobb's surveys of 1900-04.

No further tuna studies of consequence were made until the survey published by

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[1] The Japanese live-bait fishery is not included here, because the principal emphasis of this report is on tropical fisheries of the central and eastern Pacific.

[2] Research in Washington, Oregon, and British Columbia is not included here, because of the primary interest of the report in tropical fisheries.

Table 3.--Tuna catch by species, Japanese tuna longline[1] (thousands of pounds)

Year	Albacore	Bigeye	Bluefin	Skipjack	Yellowfin	Total
1952	38,952	61,774	5,663	1,475	38,357	146,221
1953	41,686	57,430	12,374	562	63,814	175,866
1954	60,131	50,883	9,914	1,025	94,702	216,655
1955	52,957	83,194	8,581	1,245	132,006	277,983
1956	50,491	96,561	20,165	950	165,774	333,941
1957	59,974	112,887	30,585	1,838	182,205	387,489
1958	85,710	150,386	28,243	2,421	170,015	436,775
1959	110,644	156,003	94,649	2,837	159,354	523,487
1960	121,563	149,098	119,294	2,925	202,083	594,963
1961	121,647	219,594	129,083	2,474	188,454	661,252
1962	158,512	235,075	72,264	3,080	216,301	685,232
1963	154,028	262,403	106,755	2,568	227,238	752,992

[1] Data are from *Annual Report on Catch Statistics on Fishery and Aquiculture*, Ministry of Agriculture and Forestry, Japanese Government. About 60 percent of the total catch in recent years has been taken in the Pacific Ocean, and the remainder in the Atlantic and Indian Oceans.

Table 4.--Tuna catch by fisheries--1952-63 (thousands of pounds)

Year	Hawaii	Eastern Pacific (U.S.)	Japan[1]	Total
1952	10,305	320,798	146,221	477,324
1953	15,361	300,791	175,866	492,018
1954	17,236	321,181	216,655	555,072
1955	12,207	269,362	277,983	559,552
1956	13,625	328,604	333,941	676,170
1957	7,988	295,035	387,489	690,512
1958	8,697	316,263	436,775	761,735
1959	14,129	268,330	523,487	805,946
1960	8,951	287,765	594,963	891,679
1961	12,277	310,970	661,252	984,499
1962	10,883	293,880	685,232	989,995
1963	9,308	310,492	752,992	1,072,792

[1] About 60 percent taken in the Pacific.

Bell and Higgins in 1939. This paper brought up to date the description of the fisheries, and included detailed tables of catch for 1928-37. It also included the first published proposal for a research program in the central Pacific, to be headquartered in Hawaii.

As interest in the central Pacific increased during the years following the Bell-Higgins report, national legislative action was stimulated. This new interest culminated in passage of the Farrington Act of 1947. Since this Act led to U.S. Federal research on tuna, it seems worthwhile to quote part of it:

> ''The Secretary of the Interior, through the Fish and Wildlife Service of the Department of the Interior, is authorized and hereby directed to conduct such fishing explorations and such necessary related work as oceanographical, biological, technological, statistical, and economic studies to insure maximum development and utilization of the high seas fishery resources of the Territories and island possessions of the United States in the tropical and subtropical Pacific Ocean and intervening areas as may be consistent with developing and sustaining such fishery resources at maximum levels of production in perpetuity and to provide for the best possible utilization thereof.''

In addition, the Act provided for cooperation with other agencies and appropriations to cover the cost of a laboratory in Honolulu together with the necessary research vessels, scientific staff, and supporting personnel.

The Honolulu Laboratory was constructed, and investigations began in 1949. For several years studies heavily stressed fishing methods, oceanography, and fishery exploration. The ''POFI'' (Pacific Oceanic Fishery Investigations) name became internationally known. Oceanographic features such as the Cromwell Current were discovered and their relation to tuna distribution studied.

More recently emphasis has shifted toward separation of races by immunogenetic studies and experimental investigation of tuna behavior and physiology. Other studies in fishery biology are being continued, and emphasis on physical oceanography continues. Skipjack catches are being predicted, and models of albacore and skipjack populations have been constructed.

Tunas in the eastern Pacific were first studied by the California Department of Fish and Game. Research that began in the early 1930's included such topics as catch analyses, systematic studies, racial separation, migrations, and age and growth. Work has continued to the present.

A convention between the United States and Costa Rica, ratified in 1950, created the Inter-American Tropical Tuna Commission (IATTC). Member nations increased to five in 1964 by adherence of Panama (1953), Ecuador (1961), and Mexico (1964). A research staff, established soon after initial ratification of the convention, has continued to be active. During its 14 years of existence the IATTC staff has compiled an impressive record of published research. Work on the dynamics of stocks of yellowfin tuna has been particularly noteworthy. Other areas of research included bait fish biology and statistics, oceanography, racial separation, larvae, and physiology.

Most recently formed of the eastern Pacific tuna research groups is the U.S. Bureau of Commercial Fisheries Tuna Resources Laboratory at La Jolla, California. Investigations have stressed forecasting of tuna catches, particularly for albacore, on the basis of sea temperatures and other variables. Other fields of study have included tuna behavior, fishery operations, biology of albacore and bluefin tuna, and general oceanography.

Research on tuna has been limited in Peru. It has been concerned chiefly with the taxonomy and biology of the bonito. Some other countries have collected statistics.

As the world's greatest fishing nation, Japan has long emphasized fishery research in her colleges, universities, and government agencies. Studies of tuna have been included over several decades and no sharp line of distinction can be drawn to separate high-seas fishery studies from inshore ones. General impressions regarding research emphasis in Japan can be gained by inspection of the papers included or cited in The Proceedings of the World Scientific Meeting on the Biology of Tunas and Related Species, issued by FAO after a meeting held in 1962. The skipjack tuna has received the greatest attention, but emphasis has been heavy also on yellowfin tuna. Less work has been done on albacore and bigeye tuna. Only a few papers have referred to bluefin tuna. This species probably will get more attention in the future, since its relative importance in the longline fishery is increasing (table 3).

Topics of research reflect Japan's traditional emphasis, as a high-seas fishing nation, on fishing methods and oceanography. Other areas that receive considerable attention included food and feeding, racial separation, and fishery dynamics. Less attention was paid, at least up to 1962, to research on age and growth, spawning and larvae, behavior, physiology, and bait fish.

Both national and prefectural units have conducted research. The Nankai Regional Fisheries Research Laboratory appears to be especially active in current research on tuna, principally on bigeye and yellowfin tunas. The Tohoku laboratory in Sendai is active in skipjack research. Recent work (1950's or later) is reported from the prefectural stations of Mie, Iwate, Kanagawa, and Miyazaki. Earlier work was attributed to the Niigata, Kagoshima, Okinawa, Shizuoka, Kumamoto, Chiba, and Oita stations.

GEAR AND ECONOMIC STUDIES

Development of Competitive Fisheries

Any general study of the abundance and yield of tropical tuna at the Honolulu Laboratory must surely envision the development of a major U.S. fishery in the central Pacific. Unless protected by tariffs, products of such a fishery would have to compete for markets with those of the existing well-developed Japanese longline fishery. Because their unit labor costs are higher, American boats will have to operate more efficiently, as purse seiners have done in the eastern Pacific. This topic is outside my field of competence, but is included for completeness. Merely as suggestions, I mention a few possibilities.

Boats might be designed to be faster and lighter by use of fiber glass or other modern hull materials. Better power plants may be feasible. Possibly types of gear could also be improved. The feasibility of electronic fishing aids, deep purse seines, mechanized longlining, and midwater trawls should be investigated. Greater application of oceanographic knowledge to fishing should be made. For any serious work toward increase of efficiency, the services of a naval architect and a gear specialist would be required.

Study of Economic Feasibility

A rational appraisal of the possibility of success in a fishery development requires a forecast of markets, prices, and other factors in the economics. The State of Hawaii Department of Planning and Economic Development has already made and reported a preliminary study in this field. The Department estimates a U.S. demand for canned tuna by 1970 that will require about 1.4 billion pounds per year of round fish. The current (1963) annual consumption is about 900 million pounds. Thus an additional market for 500 million pounds of round fish is anticipated. If Japan continues to supply 50 percent of the fish, as the Department assumes will be true, there should still be a new market for 250 million pounds of U.S.-produced fish, or over half the current U.S. domestic catch. Further research is needed on consumption patterns and trends.

The sizes of fish and kinds of tuna meat acceptable to the U.S. market should be investigated further. Wide variation in average size of individual species (skipjack tuna, range of 5-20 pounds; albacore, 20 pounds; yellowfin tuna, 60 pounds; bigeye tuna, 130 pounds) makes this topic especially pertinent. The dark color of the flesh in such species as bigeye tuna must also be considered in assessing markets, which have traditionally preferred ''light meat'' tuna. It is possible that new products, such as the fish sausages now popular in Japan, could be popularized in U.S. markets. The feasibility of introducing new products was demonstrated some years ago by the development and dramatic rise in consumption of ''fish sticks'' made from fish caught by trawl.

PROPOSED STUDY OF ABUNDANCE AND YIELD

If a large fishery is to be developed in the central Pacific as indicated above, forecasts of the supply of raw material must be as accurate as possible. The traditional estimates of maximum sustainable yield will be required, and these in turn involve most of what is currently classified under the heading of fishery biology. It will be valuable, nevertheless, to consider what specific types of data must be assembled for predictions of tuna yield.

Types of Data Required

CATCH-EFFORT DATA

Fullest possible use should be made of data from the long record of the local Hawaiian longline fishery. If possible, log books for detailed records of fishing effort should be placed aboard all boats in the fleet. Data recorded in logs should include time of departure from and return to port, estimated location of set, time of start and end of set, amount of gear set, number of hooks per basket, length of line per basket, estimated distance between buoys, and catch by species number and weight.

Detailed records of the eastern Pacific fishery are being collected by the California Department of Fish and Game, the U.S. Bureau of Commercial Fisheries, and the Inter-American Tropical Tuna Commission. Because some tunas migrate freely between the central and eastern Pacific, and because the fisheries are beginning to overlap, it is essential that exchange of data be arranged. Although data are normally retained by the collecting agency until analysis and publication, there should be no objection to furnishing the data after these processes have been completed.

Fortunately the All Japan Investigative Conference of Tuna publishes monthly summaries of catch-effort data for the Japanese longline fishery, by 5° quadrangles of latitude and longitude. The data include catches by species and effort as numbers of hooks fished. They are being further summarized by 20° quadrangles at the Honolulu Laboratory of the U.S. Bureau of Commercial Fisheries. The detailed data by 5° quadrangles are available only from 1961 to date, but data by larger, irregular areas are available for 1953-59.

Several critical studies have been made recently of variability in the catchability coefficient q in the relation $F = qf$ (where f = fishing effort and F = instantaneous fishing mortality rate). This relation is important, since the value of F in the population model is important in determining the estimated sustainable maximum yield. When the mathematical models were developed by Baranov, Ricker, Beverton and Holt, Schaefer and others, they assumed that within the fishing area either the fish or the units of fishing effort were randomly distributed, or that a reasonable approximation to such a condition existed. Studies of distribution and density of tuna schools show that the above assumptions are not even approximately true for these species. The fish are contagiously distributed, and because the fishermen engage in searching, their effort is not randomly expended, either in time or space. Special data should be gathered by areas no larger than 1° quadrangles to study variation in q. Since quantitative data on the size, density, spacing, shape, and depth of schools are needed, observations from research rather than fishing vessels will be required. These studies could be made within 20° quadrangles selected to be representative of a range of fishing intensities and geographical areas.

OTHER BIOLOGICAL DATA

Any valid biological study of fish populations requires that the stocks be defined. Within a species, geographical location or other types of separation may give rise to groups of fish that do not fully interbreed with all other members of the species (even though they are capable of doing so), and which as a result acquire distinctive genetic characteristics. A number of studies, especially those based on blood-group differentiation, have been given strong support to the idea that subgroups (''races'') exist within the several species of tuna. It is most important that the population models for estimation of yield deal with well-defined units. To this end, current studies, of immunogenetics for example, should be intensified.

In highly migratory fish like the tunas the stock units do not remain in a single geographical area. Again it becomes important to the population model to be able to follow the units from place to place and to know the shifts in their geographical distribution. Perhaps the most direct evidence can be obtained by the release and recovery of tagged or otherwise marked fish. Because of the cost of tagging at sea, however, the numbers of fish included are likely to compose such a small percentage of the population as to introduce severe sampling problems. Possibly a more practical and effective method of separating stocks is the study of blood group systems. With both methods good experimental design is essential if results are to be trustworthy. Finally, analysis of distributions of length or age, or both, may be fruitful; and again the samples can be large.

Some representation of growth in weight at the ages the fish are taken is required for all population models. A growth curve is normally deduced from average weights at age (or lengths at age combined with a weight-length relation). As mentioned below, however, direct determination of age is difficult for the tunas. Again, it seems reasonable to investigate further the length-frequency approach, perhaps supplemented with direct evidence from marking and recovery. Variation in growth rate with temperature, food supply..., should also be investigated.

The mortality rates essential to population models may sometimes be estimated from ''catch curves'' of age composition of stock units. Difficulties have been experienced in attempts to determine age from the vertebrae, scales, or other hard parts of tunas. For this reason and also because of the more effective sampling possible, the use of length frequencies for inferring mortality rates should be further investigated.

Estimates of fishing and natural mortality rates F and M are, of course, essential ingredients of any population model. The possibility of using age or size composition to estimate total mortality Z has been mentioned above. This datum might also be estimated by tagging. Since $F + M = Z$, it is necessary to have an estimate of either F or

M in addition to Z. Again, tagging or marking and recovery offer one approach to estimates of F: analysis of statistics, another. A method has been developed for rough estimates of M from growth-curve constants and lifespan.

Finally, some information must be gained about the relation between population size and subsequent recruitment to the commercially fished stock. The currently popular ''yield per recruit'' estimates give no indication of potential sustained yield unless something is known of the expected rates of recruitment. Information on total stock size might be gained from tagging or egg or larval surveys, although the identification of the eggs of some tunas still has not been accomplished. Estimates of population size may also be deduced from catch-effort data in conjunction with data on size and age, by appropriate analysis as indicated above.

The estimates so gained can then be related to recruitment to the commercial stock, at whatever age it occurs. Some estimate is needed of the size of the first (or first important) age group in the fishery. Age determinations may be available from direct reading of hard parts, or from analysis of length frequencies. When weighted according to abundance, age distributions provide estimates of recruitment to relate to the size of the parent population.

ENVIRONMENTAL DATA

Because tunas spend their entire lives in the open sea, variations in the oceanic environment may be assumed to have profound effects on their growth, survival, distribution, and vulnerability to capture. For instance the stock-recruitment relation and adult natural mortality (M) may be drastically altered by major changes in sea temperatures, currents.... As was true for economics, I am here speaking about a field largely outside my own training and experience.

Appropriate adjustments of yield predictions from population models require some predictions of ocean climate. Required in turn are continued and intensified studies of water mass movements, air-sea interaction, and the like. Ships must continue to go to sea and make the standard measurements of temperature, salinity, oxygen concentration, light penetration, abundance and distribution of plankton, and distribution of tuna eggs and larvae. Synoptic analyses should cover the entire Pacific range of the tunas, and data from several collecting agencies should be pooled.

When satisfactory environmental indices are available, they can be compared with anomalies of tuna abundance from that predicted by conventional models. This procedure could lead to the development of a refined model of cause and effect which could then be tested by further observations and experimentation.

Mechanics of Abundance-Yield Study

The purpose of a study of abundance and yield can be no other than to make some prediction about the future. These predictions may be for individual fishing seasons, or they may merely anticipate the average yield levels (particularly maximum levels) that may be expected under certain average levels of fishing intensity. A number of types of useful models are considered below.

SINGLE SPECIES MODELS

Most of the classical fishery models have been of the single-species, deterministic type. Analytically determined formulations develop single-valued expressions of yield as a function of fishing and natural mortality and growth rates and age at entry. Most of these have given answers in terms of "yield per recruit." They may be made more general by including a stock-recruitment relation, to provide a specific yield estimate for each fishing level. Although models may be generated on a desk calculator, use of an analog or digital computer saves much time.

Models may be improved further by employment of stochastic rather than deterministic formulas. These approaches allow for statistical variation in mortality and in rates of growth and recruitment, as occurs in nature. The great complexity of stochastic models probably dictates the use of a digital computer if they are to be generated in any reasonable period of time. Results permit the assessment of confidence limits about the predicted yields, something of especial value where economic stakes are large.

MULTIPLE SPECIES MODELS

Since two or more species of tuna or other similar fish often occupy the same area, competition for food and other interactions are highly likely. Such situations require going beyond the conventional models mentioned above. The differential equations of Volterra provide for simple types of species interaction, and may be used at least as a point of departure. For a deterministic treatment the analog computer is well adapted to generation of the Volterra functions for two or three species.

A realistic appraisal will probably reveal situations in which three or more species interact with each other. Formulations have not to my knowledge been developed for such situations. Models obviously would be extremely complex, and use of a digital computer would be required.

COMPLETE MODELS

It may be possible eventually to construct complete stochastic models of the tunas, their predators, competitors and forage organisms, and their physical environment. The large number of variables included in such models may make it extremely difficult to attain unique and trustworthy results. A degree of freedom is lost for each new variable that is introduced; consequently long series of observations are required. Although such models may sound fanciful at the present "state of the art" in tuna research, their possibilities should not be overlooked. Digital computers obviously would be essential for such complex models.

YIELD PREDICTIONS

When valid population models have been constructed, they can be used to predict yields of the several species of tuna at given fishing intensity and under given environmental conditions. If environmental variables can be considered to "average out" over a period of several years, average yields for such periods can be computed for a range of fishing intensities. The results will be "yield isopleths" of the types found in Beverton and Holt. If the maximum sustainable yield is desired, the fishing intensity and age of entry corresponding to it can be determined from the isopleths.

Yield predictions for individual years would be of obvious value to the fishing industry. They would require considerably more precise data than are needed for the average predictions described above. Nevertheless, preseason forecasts for individual years have been made with some success for certain species and localities. An example is the series of forecasts of albacore catch issued by the Tuna Resources Laboratory at La Jolla, California, and the forecasts for skipjack tuna issued by the Biological Laboratory, Honolulu.

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DISEASES OF MARINE FISHES

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> " One of the most serious gaps in our knowledge of marine ecology is the study of diseases . . . epidemics are common occurrences in marine environments. . . . They may be an important cause of fluctuations, and should therefore have a prominent place in research programs."
>
> Lionel A. Walford, " Living Resources of the Sea ",
> Ronald Press Company, 1958, p. 147.

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I. Introduction

Research commitment to the study of marine fish diseases has been until recently sporadic and inadequate. Although knowledge of fresh-water fish diseases has proliferated, especially in hatcheries, little incentive has existed for comparable investment in understanding the ills of marine species. The vastness of the oceans, the complexity of natural factors regulating the size of fish populations, and the lack of methods to control and manipulate such factors, have tended to discourage continuing and extensive studies of such specific aspects of the marine environment as disease. Growing awareness that the human population is increasing enormously, that over two-thirds of the earth's surface is ocean, and that we understand little of the dynamics of production in the sea, has led to increasing scrutiny in recent years of those variables that might at any particular time become overriding in their influence on population size. Disease is one such variable.

Diseases of food fishes have logically received greatest attention in past research, and will do so in the present paper. Parasites and diseases, in addition to killing the host, can materially reduce the value of fish as food for humans; this fact serves as a further incentive to examine diseases of commercial species. Non-utilized fish may receive attention because of some academic interest, but the preponderance of research concerns food species with large biomass. The term " disease " is used here in its broadest possible sense, to include any departure from normal structure or function of the organism—encompassing those states that result from activities of infectious agents, parasite invasion and genetic or environmentally induced abnormalities. Such a broad definition of disease in marine fishes requires the inclusion of a surprising amount of widely scattered literature—probably more than can be comfortably considered in this review, and certainly more than might be expected in view of the apparent neglect of the field.

Access to the literature on marine fish diseases is at present indirect. Several general texts on fish parasites and diseases have appeared in the German language (Hofer, 1904; Plehn, 1924; Schäperclaus, 1954; Amlacher, 1961). The latest edition of Schäperclaus' excellent text contains information on disease in marine as well as fresh-water fishes. Recently, several shorter texts on diseases of lower vertebrates by Reichenbach-Klinke have been translated into English, expanded, and combined into a more comprehensive work (Reichenbach-Klinke and Elkan, 1965). Kahl, Reichenbach-Klinke, and Schäperclaus have made numerous significant contributions to the German literature. Russian texts, symposium volumes and reviews (Liaiman, 1949, 1957; Dogiel, 1954, 1955; Petrushevskii, 1957; Dogiel *et al.*, 1958; Pavlovskii, 1959, 1962; Polyanski and Bykhovskii, 1959) contain summarizations of marine studies and have appeared in English translations. Among the important contributors to the Russian literature have been Dogiel, Petrushevskii, Polyanski and Shulman. Other nations have also made significant summarizing contributions to the general literature on fish diseases. Bergman (1923) published an early monograph in Swedish; Fujita (1943) published a text on diseases of fish and shellfish in

Japanese; Davis (1953) published an English language text on culture and diseases of fresh-water game fishes; and Ghittino (1963a) recently published a handbook in Italian. A symposium on fish diseases held at Turin, Italy, in 1962 has been published by the Office International des Epizooties (Altara, 1963). English-language reviews and symposia on selected aspects of fish-disease research, usually including references to marine diseases, have appeared (Kudo, 1920, 1924, 1933; Sproston, 1946; Nigrelli, 1952a; Oppenheimer and Kesteven, 1953; Snieszko, 1954; Manter, 1955; Hoffman and Sindermann, 1962, Oppenheimer 1962; Sindermann, 1963; Post, 1965; Putz *et al.*, 1965; Snieszko *et al.*, 1965). Texts which include considerations of marine fish diseases and parasites include: Breed *et al.* (1957)—bacteria; Johnson and Sparrow (1961)—fungi; Kudo (1954)—protozoa; Yamaguti (1958–63)—helminths; Dawes (1946, 1947) and Skrjabin (1947–62)—trematodes; Wardle and McLeod (1952)—cestodes; and Yorke and Maplestone (1926)—nematodes. Johnstone, Kabata, Linton, Nigrelli, Snieszko and Templeman are among those who have made important contributions to the English and American literature.

The general plan of this paper is to consider examples of the significant diseases of marine fishes, concentrating sensibly on those that have received somewhere near adequate scientific attention, and attempting to include those caused by a wide variety of pathogens and parasites. In the necessary process of selection at least two things happen: (1) many examples and much literature must be neglected or not treated in sufficient depth, and (2) a natural tendency arises to choose examples close at hand or drawn from the author's research. Thus, illustrative material has been taken to a large extent from studies in the North Atlantic, although comparable material could be obtained from other geographic areas. Omitted is much of the great but scattered fund of published information from parasite surveys, including a large part of the ecological parasitology of the USSR, which has been effectively summarized by Dogiel *et al.* (1958). Many descriptions of occasional parasites of fishes have not been considered, even though effects of such parasites may be properly included in the broad definition of disease used in this paper. The literature cited thus includes only a small part of the often extensive published information on any particular parasite group. The references, extensive as they may seem, represent a too-small sampling of the world literature. This is particularly true of the older literature, which for groups such as the Myxosporidea and Microsporidea is voluminous and elaborate. References to some of the early literature have been compiled by McGregor (1963); access to other early work can be gained through bibliographies included in more recent papers. For such parasite groups as the haemogregarines, the monogenetic trematodes, the cestodes, the nematodes, or the parasitic copepods, the consideration in this paper therefore represents only a tiny, but hopefully a representative, fraction of the whole.

Diseases of estuarine and anadromous species are included, as well as those of species that are strictly marine, except that treatment of anadromous fishes is limited to situations where the pathogen or parasite is of marine origin. Diseases of fishes from saline inland seas have been considered, since many of the hosts and their parasites are of marine origin. Many of the diseases discussed are characteristic of inshore or estuarine waters, where abnormal conditions are more readily noted and examined than in the open sea. Fish carcasses washed up on beaches or floating in shoals near shore are much more likely to elicit action, scientific or otherwise, than would similar events a hundred miles from shore. Also, scientific studies of marine animals in the past have often varied inversely with distance from the shore. As a result, much of the world literature on fish diseases concerns inshore events.

II. Microbial Diseases

Included in the category of " microbial diseases ", and aggregated here largely for convenience, are those of viral, bacterial, fungal and protozoal etiology. They include the infectious diseases of fishes, caused by parasites capable of destruction of host tissue and multiplication within the fish. Resultant pathology and the course of disease may depend on such factors as infective dose, virulence and resistance of the individual host animal as well as host nutrition and other environmentally influenced variables (Snieszko, 1957a, 1964). The disease condition may range from chronic to acute, with varying degrees of host response.

A. *Viruses*

Virus diseases of marine fishes, although not unknown, are not reported abundantly in the scientific literature. Much of this lack of knowledge probably stems from the absence, until recently, of adequate techniques for study. With the successful establishment of fish cells in culture (Wolf and Dunbar, 1957; Clem *et al.*, 1961; Wolf and Quimby, 1962), a most important tool has become available, and understanding of the role of viruses in marine fish populations should increase greatly in the next decade. Viruses are best known in marine fishes as suspected or known etiological agents of several neoplastic, hyperplastic and hypertrophic diseases. Lymphocystis disease and certain papillomas have long been felt to be of viral origin, based on epizootiological and transmission studies, and on the presence of inclusions in affected cells.

Lymphocystis is probably the best known virus disease of marine and fresh-water fishes. First described from the European flounder, *Pleuronectes flesus* (L.),* by Lowe (1874), and soon after from other species (McIntosh, 1884, 1885; Sandeman, 1892; Woodcock, 1904), the disease has since been reported from the orange filefish, *Alutera schoepfi* (Walb.), by Weissenberg (1938) and Nigrelli and Smith (1939); the killifish, *Fundulus heteroclitus* L., by Weissenberg (1939a); the red mullet, *Mullus surmuletus* (L.), by Alexandrowicz (1951); and from other marine and fresh-water species (Smith and Nigrelli, 1937; Weissenberg *et al.*, 1937; Weissenberg, 1945). Recently several cases of presumed lymphocystis in striped bass, *Roccus saxatilis* (Walb.), have been observed (Anonymous, 1951; Sindermann, unpublished). The disease was originally thought to be caused by parasitic protozoa or eggs of another animal laid under the skin of fish (Sandeman, 1892; Woodcock, 1904). Weissenberg (1914, 1920) and Joseph (1918) were the first to recognize lymphocystis cells as hypertrophied fibroblasts. Transmission studies (Rašín, 1927, 1928; Weissenberg, 1939b, 1951b; Wolf, 1962) have demonstrated the infectious nature of the disease and have suggested some degree of host specificity. Definitive evidence that a virus is responsible for lymphocystis was obtained by electron microscopy (Walker, 1962; Walker and Wolf, 1962) and by transmission of the disease with ultracentrifugates and bacteria-free filtrates (Weissenberg, 1951a; Wolf, 1962). Manifestations of lymphocystis include whitish nodules on body and fins caused by hypertrophy of fibroblasts and osteoblasts (Fig. 1a). The connective tissue cells grow to enormous size (5 mm in some cases) and become surrounded by a thick hyaline capsule. In severe cases most of the body surface may be involved. Weissenberg (1921a) reported that in some areas up to one-third of a population of fish could be affected. A great body of literature has accumulated on lymphocystis, and much of the early work was well summarized by Nigrelli and Smith (1939). A history of research on the disease has just been published (Weissenberg, 1965).

A recent and apparently sharply defined outbreak of lymphocystis

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* Throughout the paper an attempt has been made to give common and scientific names of fishes when they are first mentioned, and only the common name thereafter. In some cases this is not possible, as for example when the same common name is applied to several different species in different geographical areas, or when a species may have a different common name in different areas. Scientific names of fishes from North American waters follow the recommendations of the American Fisheries Society (1960).

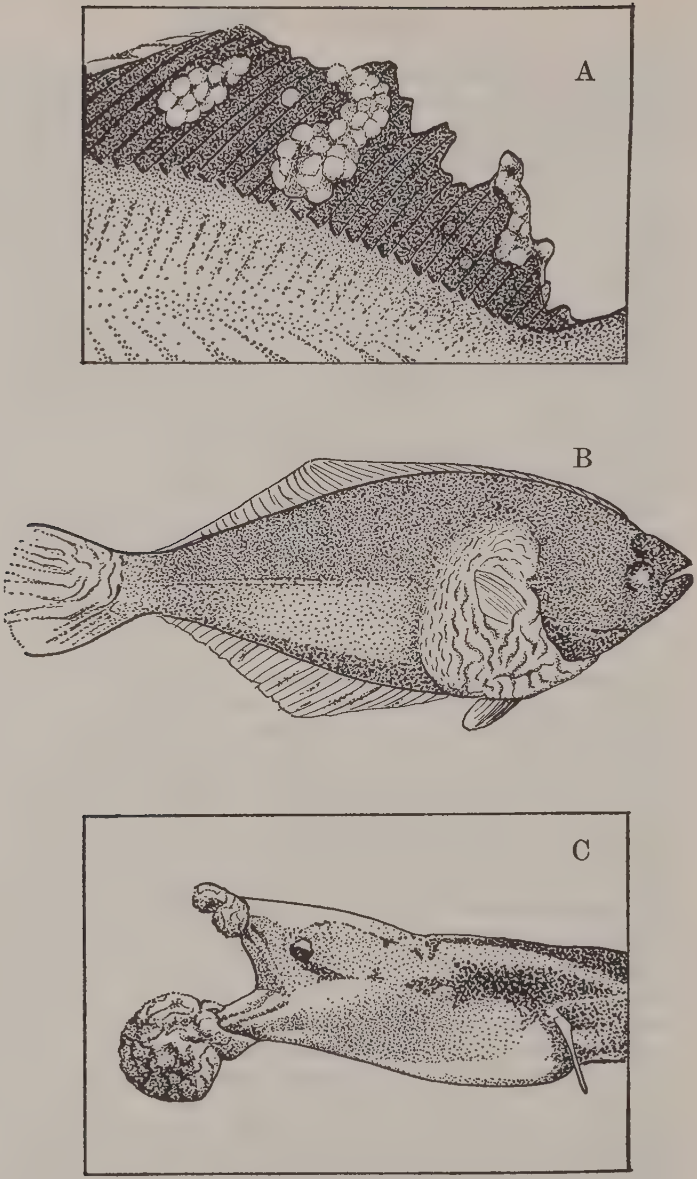

FIG. 1. (*a*) Lymphocystis disease of the dorsal fin;
(*b*) papilloma of flounder;
(*c*) cauliflower disease of eel.

in American plaice, *Hippoglossoides platessoides* (Fabr.), of the Grand Bank was reported by Templeman (1965b). Infected fish were first seen in 1960, and in 1964 the infection level in American plaice on the eastern slope of the Grand Bank was approximately 1%. Badly infected fish, called " scabby " or " seedy " by fishermen, were thrown overboard, and estimates of such discards ran as high as 300–400 pounds per set in areas of heavy infections. Trawlers usually moved to other locations where fewer fish were diseased. Templeman suggested several possible explanations for the outbreak, including the possibility that the disease is enzootic in the population and may increase in intensity periodically. Nordenberg (1962) found infections as high as 12% in flounders, *Pleuronectes flesus*, from the Öresund, with some indication of higher prevalence in the warmer months of the year.

Neoplastic or hyperplastic diseases, some thought to be of virus origin, include dermal and epidermal papillomas of many flatfish species (Fig. 1b). Such diseased conditions have been reported from: halibut, *Hippoglossus hippoglossus* L., by Johnstone (1912a); plaice, *Pleuronectes platessa* (L.), by Johnstone (1925); sole, *Solea solea* (L.), by Thomas (1926); winter flounder, *Pseudopleuronectes americanus* (Walb.), by Smith (1935); flathead sole, *Hippoglossoides elassodon* Jord. and Gilb., by Wellings and Chuinard (1964) and Wellings *et al.* (1964); as well as from other pleuronectids. Suspected viral particles have been described from the cytoplasm, but transmission has not been reported. Similar epidermal hyperplasia, of suspected viral etiology, is common in fresh water among European cyprinids. Characterized by irregular white raised patches on the skin, the disease is often referred to as " fish pox " (Roegner-Aust and Schleich, 1951; Roegner-Aust, 1953).

A remarkable tumorous growth of eels is aptly labelled " Blumenkohlkrankheit " or " cauliflower disease " (Fig. 1c). This common chronic fibro-epithelial tumor, often of dramatic proportions, occurs principally in the head region of European eels, *Anguilla anguilla* (L.). Reports of the disease in European rivers and coastal waters have increased in recent years (Schäperclaus, 1954; Lühmann and Mann, 1957; Engelbrecht, 1958). Transmission has not yet been effected, but virus etiology is strongly suspected (Christiansen and Jensen, 1950). Eels with progressive tumors become emaciated and die. Schäperclaus (1953a) also found comparable growths in cod, *Gadus morhua* L., and papillomas have been reported from smelts, *Osmerus eperlanus* (L.), taken in the Baltic Sea with characteristics very similar to cauliflower disease of eels (Breslauer, 1916).

A number of highly pathogenic viruses of fresh-water fishes do not cause tumors (Wolf, 1964). The diseases produced include infectious stomatitis in fishes from South American rivers (Torres and Pacheco, 1934; Pacheco, 1935), viral hemorrhagic septicemia of salmonids in Europe (Jensen, 1963), and infectious pancreatic necrosis of trout, *Salvelinus fontinalis* (Mitchill) and *Salmo gairdneri* Richardson (Wolf *et al.*, 1960). Among the anadromous species, viral etiology has been indicated for a disease of chinook salmon, *Oncorhynchus tshawytscha* (Walb.), from the Sacramento River, California (Ross *et al.*, 1960; Parisot and Pelnar, 1962), and for a more widespread disease of sockeye salmon, *Oncorhynchus nerka* (Walb.), in the Pacific Northwest (Watson *et al.*, 1954; Guenther *et al.*, 1959). Transovarian transmission was hypothesized for the chinook disease, and the feeding of fingerlings with diets including salmon carcasses was implicated in the sockeye disease. The discreteness of the viruses involved, and the pathological changes in host tissue, have been summarized by Parisot *et al.* (1965) and Yasutake *et al.* (1965).

Viruses that do not cause tumors have not yet been clearly demonstrated in marine fishes. Moewus (1963) reported studies of a ciliate parasite, *Miamiensis avidus* Thompson and Moewus, which was isolated from tumor-like nodules on seahorses, *Hippocampus erectus* Perry. The organism was studied as a possible vector of virus; polio virus was used in absence of a suitable laboratory strain of marine virus. Results were inconclusive, but the author's suggestion of parasites as possible vectors of fish viruses does not seem unreasonable; in fact it was made previously by Thomas (1931) and Nigrelli (1948) in reference to epidermal hyperplasias of cyprinids. Transmission of viral and rickettsial agents by parasites is known for certain diseases of mammals (swine influenza and salmon poisoning of dogs). Moewus-Kobb (1965) also reported that virus of infectious pancreatic necrosis of fresh-water fishes multiplied when introduced into cell cultures derived from a marine fish, the grunt, *Haemulon sciurus* (Shaw). The same cell line of grunt was found to harbor a presumed " orphan virus " destructive to primary explants as well as fish cell lines (Clem *et al.*, 1965).

B. *Bacteria*

Reports of bacterial epizootics in marine fishes are surprisingly infrequent, and in fact relatively few bacterial pathogens have been recorded from natural populations of marine fishes. This is probably due to lack of observation or to inadequate examination rather than lack of occurrence. Two examples support this view. Oppenheimer and Kesteven (1953) reported underwater observations of fish schools in which up to 10% of individuals exhibited lesions indicative of bacterial infections later demonstrated by smears and cultures. Sindermann and

Rosenfield (1954a) in their study of bacterial tail rot of Atlantic herring, *Clupea harengus* L., reported observation of typical disease signs in schools of immature fish from the Maine coast (Fig. 2).

Among the widespread bacterial epizootics, one caused by a species of *Pasteurella* resulted in extensive and selective mortalities of white perch, *Roccus americanus* (Gmelin), and to a lesser extent striped bass in Chesapeake Bay during the summer of 1963 (Snieszko *et al.*, 1964). The pathogen was isolated consistently in pure culture from moribund white perch, and was identified as a member of the genus *Pasteurella* on the basis of morphology and biochemical tests. Catch statistics and unpublished observations by the author in 1964 suggested that significant population decimation had resulted from the epizootic. This is a very recent and as yet only partially documented example of a severe epizootic which undoubtedly has its counterparts caused by other bacterial pathogens in various parts of the world. Most of these outbreaks, because of location, or because they may not involve food fish, probably escape scientific scrutiny, and are viewed by local inhabitants with the same dismay and bewilderment that must have characterized the great human plagues and epidemics of past centuries.

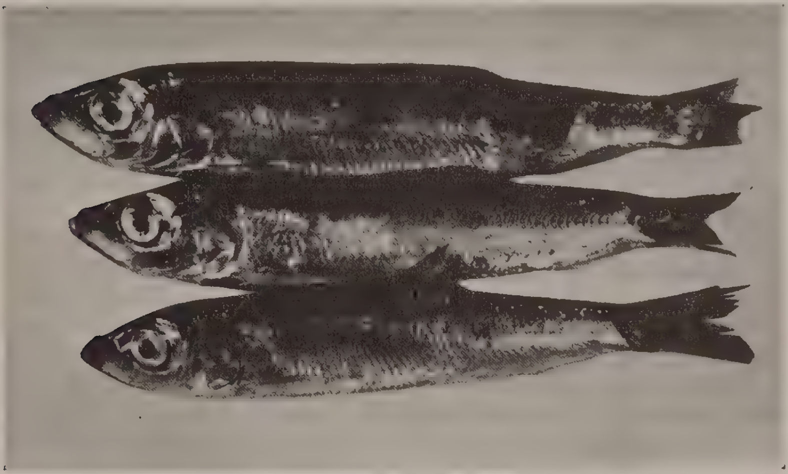

FIG. 2. Bacterial tail rot in juvenile Atlantic herring.
(From Sindermann, 1963.)

Of all the known bacterial diseases of marine fishes, none has a longer or more fascinating history than the " red disease " of eels, caused by *Vibrio anguillarum* Bergman. The disease occurs during the warmer months in brackish and salt water; reports have been most numerous from the Danish, German, Italian and Swedish coasts, and the Baltic and North Seas. According to Hofer (1904), the disease was known and reported as early as 1718 from the Italian coast, and extensive epizootics occurred repeatedly during the nineteenth century (reports date from 1825, 1850, 1864, 1867, 1884, 1885, 1889 and 1892). Signs of red disease include progressive reddening of fins and skin, visceral hemorrhages, reduced activity and death—often preceded by loosening and fraying of the skin.

The term " red disease " was introduced by Feddersen (1896) in reporting an outbreak of the disease in Scandinavian waters. Comparable outbreaks have occurred repeatedly to the present time (Feddersen, 1897; Bergman, 1909; Bruun and Heiberg, 1932, 1935; Ljungberg, 1963), often causing significant mortalities and economic losses. The disease has also been reported from The Netherlands (Schäperclaus, 1927), Poland (Kocylowski, 1963), and Germany (Schäperclaus, 1934; Mattheis, 1960). Characteristically, infections become evident among eels stored, even for short periods, in live boxes. Dead eels may be found in nets, traps and impoundments during epizootics—the disease apparently spreads very rapidly among captive fish.

An extensive survey was conducted by Bruun and Heiberg (1932) documenting the widespread occurrence of the disease in Scandinavian waters at the time, and providing information about previous outbreaks dating back to 1880—outbreaks which sometimes brought the fishery to a standstill.

Vibrio anguillarum appears to be a truly marine pathogen, limited to salinities above 9 ‰ and unable to survive in fresh water. Infection may occur through gills or digestive tract. Its effect is most pronounced and mortalities are most common in late summer, in areas where sea temperatures exceed 16°C.

Bruun and Heiberg raised new questions in their report on the 1931 epizootic in Danish waters by suggesting that several pathogens may be involved in red disease from different geographic areas. They pointed out that only a few of the early studies (Canestrini, 1893; Inghilleri, 1903; Bergman, 1909) included bacterial examinations, and that at least three bacterial disease entities may be involved in salt water. Schäperclaus (1930) also demonstrated that red disease of eels in fresh water may be caused by *Pseudomonas* (*Aeromonas*) *punctata* Zimmerman. Other observations suggest that reddening of the skin of eels may be a generalized response to abnormal temperatures and reduced availability of oxygen, as well as to bacterial invasion. There seems little doubt, however, that a common infectious agent is involved in many of the outbreaks reported, since *Vibrio anguillarum* has been isolated repeatedly (Bergman, 1909; Schäperclaus, 1927; Nybelin, 1935b). Two types, A and B, of the *Vibrio* have been identified, and a toxin has been demonstrated. *V. anguillarum* has also been found to be pathogenic to cod and plaice (Dannevig and Hansen, 1952; Bagge and Bagge, 1956; Ljungberg, 1963), pike (Schäperclaus, 1928; Ojala, 1963), and trout, *Salmo trutta* L. (Smith, 1961).

Other *Vibrio* diseases of marine and fresh-water fishes have been reviewed by Rucker (1959). He suggested that *Vibrio* infections may be much more prevalent than had been previously recognized, pointing out as examples that *Vibrio* infections often kill Pacific herring, *Clupea pallasi* Val., held as live bait, and that a study by Bückmann (1952) disclosed that almost half of a sample of 117 European plaice had natural *Vibrio* infections.

Bacterial dermatitis, sometimes accompanied by ulcerations and fin rot and usually associated with *Pseudomonas*, has been reported from wild populations of marine fishes. *Pseudomonas ichthyodermis* infections have been observed by Wells and ZoBell (1934), ZoBell and Wells (1934), and Hodgkiss and Shewan (1950). ZoBell and Wells reported evidence of the infection in killifish, *Fundulus parvipinnis* Girard, in their natural habitat on the Pacific Coast, and stated that 90% of these fish died of the disease when brought into aquaria during the summer. Other species, such as gobies, *Gillichthys mirabilis* Cooper, blennies, *Hypsoblennius gilberti* (Jordan), and smelt, *Atherinops affinis* (Ayres), also exhibited lesions. Characteristics of the disease included an initial whitish spot on the body surface which expanded rapidly, disintegration of melanophores, raising and sloughing of scales, minute hemorrhages and death. Smears from lesions revealed almost pure cultures of *Pseudomonas ichthyodermis*, but there was no evidence of systemic invasion, nor could the organism be demonstrated in the blood. Reinfections from cultures were made repeatedly; initial lesions occurred within 18 hours and death within 14 days. Mortality of fish infected from cultured pathogens was not as high as that of fish infected directly with material from lesions. The pathogen was described as a motile, Gram-negative, non-spore-forming, halophilic bacillus, with a temperature optimum for infectivity, growth and virulence in the region of 20°C. A significant finding was that fish kept in water above 30°C did not become infected and that badly diseased fish recovered rapidly if acclimated successfully to water of 32–35°C.

Hodgkiss and Shewan (1950) described an intramuscular lesion in plaice and obtained presumptive evidence that *Pseudomonas ichthyo-*

dermis was the etiological agent. More recently, Shewan (1963) has suggested that the pathogen should be placed in the genus *Vibrio*.

Tuberculous lesions with acid-fast bacilli have been reported from a number of commercial marine fishes, including halibut (Sutherland, 1922; Johnstone, 1927; Hodgkiss and Shewan, 1950), cod (Alexander, 1913; Johnstone, 1913), and plaice (Hodgkiss and Shewan, *op. cit.*). Spontaneous lesions of this type in marine fishes have been thought until recently to be rare, so that single cases have warranted descriptions in the literature. Aronson (1926) characterized and named *Mycobacterium marinum* from several species of marine fishes, including Atlantic croaker, *Micropogon undulatus* (L.) and sea bass, *Centropristes striatus* (L.), in the Philadelphia Aquarium; this remains as the only fully-characterized *Mycobacterium* of marine fish origin, although others are known to exist and have been partially characterized (Alexander, 1913; Sutherland, 1922; Griffith, 1930; Reichenbach-Klinke, 1955c). Aronson (1938) pointed out that mycobacteria responsible for spontaneous tuberculosis in marine fishes differed from acid-fast bacilli known as human pathogens, but the classification of pathogenic mycobacteria is at present very confused (McMillen and Kishner, 1959; McMillen, 1960; Nigrelli and Vogel, 1963). A recent review by Vogel (1958) reported acid-fast bacillus disease, principally in the form of visceral lesions, in 120 species of marine and fresh-water teleosts throughout the world. Parisot (1958) has also reviewed the literature on tuberculosis in fish. He suggested that this disease may be serious for adult Pacific salmonids, and that it may be partly responsible for recent decreases in the catch. Wood and Ordal (1958), Ross *et al.* (1959), and Ross (1960) found high prevalence of tuberculosis in salmon returning from the sea, but attributed much of it to early exposure to bacilli in hatchery diets which included carcasses of tuberculous fish. Walford (1958) listed tuberculosis as a disease of young Pacific salmon, and felt that the pathogen may have been acquired in the sea. Infected fish were characterized by reduced growth, incomplete gonad development, and kidney lesions containing acid-fast bacilli.

In addition to tuberculosis, Walford considered several other interesting bacterial diseases of young Pacific salmon from salt water. (1) “ Hemorrhagic septicemia ” occurred repeatedly and caused extensive mortalities in young salmon held in salt water. Outbreaks were found to be caused by a *Vibrio* enzootic in Pacific herring, and thought to be responsible for outbreaks and mortalities in herring and sardines, *Sardinops sagax* (Jenyns), of the Pacific Northwest. Other organisms, such as *Pseudomonas* (*Aeromonas*) *punctata* have been reported to cause hemorrhagic septicemia in fresh-water pond fishes.

(2) " Eye disease " of salmon, cod and other bottom fishes was also caused by a *Vibrio*. The disease was characterized by initial destruction of the eyes, followed by bacteremia and death. This malady may be similar or identical to " Augenkrankheit " of North Sea cod (Bergman, 1912). (3) " Boil disease " was found to be a progressive and highly fatal disease of young salmon, characterized by muscle abscesses. The pathogen was a diplobacillus resembling the causative agent of kidney disease of salmon in fresh water. (4) A myxobacterial disease similar to " columnaris disease " of fresh-water salmonids was characterized by development of gray-white lesions anterior to the tail. The lesions progressed with sloughing of skin and fins. The myxobacterium *Chondrococcus columnaris* (Davis) Ordal and Rucker, 1944, has been described as infecting skin, gills, and fins of *Fundulus heteroclitus* (Nigrelli and Hutner, 1945) and other marine species (Davis, 1922; Garnjobst, 1945).

This array of infectious diseases, either of salt water origin or enhanced by salt water phases of the life history of salmon, indicates the possibilities for disease studies in this and other anadromous fish (Rucker *et al.*, 1954).

Critical problems in the study of bacterial pathogens of fish, as may be deduced from the preceding, are the correct identification of the infectious agent and the determination of its role as primary or secondary invader. Not only is bacterial classification confused (Krasilnikov, 1949; Breed *et al.*, 1957; Prévot, 1961), but type cultures may be unavailable, and often biochemical and physiological characterization is incomplete. Bullock (1961, 1964) has made important contributions to the systematization of methods to identify bacterial pathogens in fresh water and Colwell and Liston (1960), Shewan (1961, 1963), Shewan *et al.* (1954, 1958, 1960), and Scholes and Shewan (1964) have attempted similar systematization for marine bacteria. Bacterial pathogens most commonly reported from sea fishes are species of *Pseudomonas*, *Vibrio* or *Mycobacterium*. Many of the bacteria normally present in sea water, or on the surface of fish, can invade and cause pathological effects if fish are injured or subjected to other severe environmental stresses.

C. *Fungi*

The role of fungi in the oceans has been admirably summarized in a recent book by Johnson and Sparrow (1961). Fungus diseases of marine organisms received excellent coverage by the authors, and it is startling to note that with the single exception of *Ichthyophonus hoferi* (Plehn and Mulsow)—often referred to as *Ichthyosporidium* *hoferi*—which is discussed in detail in various sections of this paper, fungus diseases of marine fishes are almost unknown.

Half a century of sporadic study in Europe and North America has provided evidence that one of the most serious fungus pathogens of fishes, marine or fresh water, is *Ichthyophonus hoferi.* Systemic infections, found in mackerel in England (Johnstone, 1913; Sproston, 1944), rainbow trout in Germany (Plehn and Mulsow, 1911), herring and mackerel in Canada (Sindermann, 1958), can result in widespread mortalities in these and other species. Epizootics of the disease are characteristic of herring, *Clupea harengus,* of the western North Atlantic (Cox, 1916; Fish, 1934; Scattergood, 1948). Six such outbreaks have been reported since 1898 (Sindermann, 1963). Drastic reduction in herring abundance due to disease has been documented, and the postulation made that this disease may be the most important single limiting factor to population growth of herring in the western North Atlantic.

Whether a single species, or a complex of related forms (Schäperclaus, 1953b; Sprague, 1965), *Ichthyophonus* is known as a menace to aquarium fishes in Europe (Lederer, 1936), as an introduced pathogen in trout hatcheries of western United States (Rucker and Gustafson, 1953), as a long-recognized pathogen of wild salmonids in western Europe, and as a pathogen of many other marine and fresh-water fishes. Reichenbach-Klinke (1954, 1955a) has assembled a list of more than 80 species that have been found to be infected by the fungus.

The disease is systemic, with foci of infection in the heart, viscera and lateral somatic muscles (Fig. 3). A simple sequence of life history stages, described from herring (Sindermann and Scattergood, 1954), involves multiple germination of heavy-walled spores, hyphal invasion of host tissues, formation of " hyphal bodies " and sequential germination of these entities. The disease has been reported in Atlantic herring in chronic and acute phases. Acute infections were characterized by massive tissue invasion, necrosis and death within 30 days. Chronic infections exhibited cell infiltration, progressive connective-tissue encapsulation of spores and accumulation of melanophores. The disease was rarely arrested completely, however, and deaths occurred in most fish within six months. During the most recent epizootics, infections averaged about 25% of all herring sampled, and many cases were acute. Enzootic prevalence was usually well under 1% and infections during this phase have been chronic in all cases examined.

Transmission of the disease has been achieved by feeding massive spore doses, derived either from cultures or from diseased fish. Increase of experimental spore doses resulted in increasing numbers of chronic infections and, beyond a certain dosage, the appearance of acute infections (Sindermann, 1963). Experimental epizootics that have been produced in large sea water aquaria duplicate many of the events observed in nature. Herring varied individually in responses to identical spore doses; some acquired acute infections, some acquired chronic infections, and some remained uninfected.

A more complex life cycle for *Ichthyophonus* has been described from mackerel by Sproston (1944). This is the only study in which indications of sexual reproduction, in the form of hyphal fusions, were observed. Other authors have described the occasional appearance of conidia-like bodies, and the occurrence of macro- and micro-hyphae. Reichenbach-Klinke (1956a) and others have raised the question of several possible species, but definitive culture studies have yet to be carried out. Reichenbach-Klinke (1956b, 1958) found *Ichthyophonus* to be very common in Mediterranean fish.

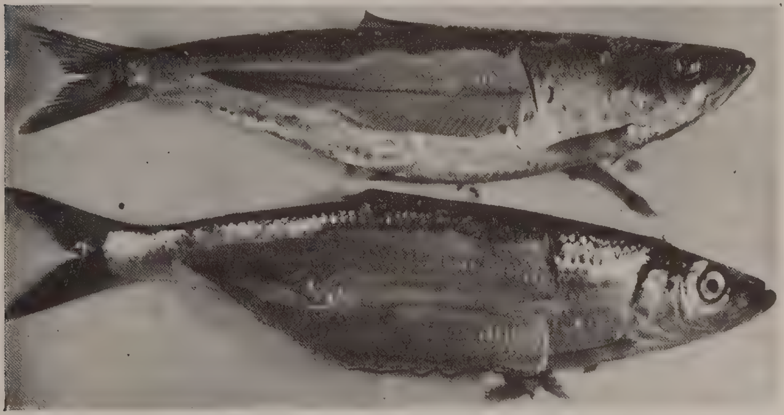

FIG. 3. Invasion and destruction of lateral body muscles of Atlantic herring by *Ichthyophonus hoferi*. Fish dissected to show normal muscle (top) and necrotic muscle in acute infection (bottom).

Other than *Ichthyophonus*, reports of fungus pathogens of marine fishes are scarce in the scientific literature. Reichenbach-Klinke (1956c) briefly described a species of *Cladosporium* found associated with hypertrophy of the epithelium of a cod, *Gadus morhua*, taken in the North Sea, but the disease is apparently rare. Reichenbach-Klinke also mentioned briefly a *Cladosporium* from the body cavity of two South American species of the genus *Hyphessobrycon* that may be found in brackish water. Apstein (1910) described infection of lumpfish, *Cyclopterus lumpus* (L.), by *Cycloptericola marina.* Cysts containing the fungus were found in the stomach wall of over half the specimens examined.

It is not uncommon for diseases and parasites of fresh-water origin, including fungi, to be carried downstream with the anadromous host to the estuary and the sea, where survival is often limited. Such appears to have been the situation in the observation of Aleem *et al.* (1953) of *Isoachyla parasitica* in *Atherina riqueti* in southern France. Similar external symptoms of fungus invasion have been seen in alewives, *Alosa pseudoharengus* (Wilson), and smelts, *Osmerus mordax* (Mitchill), as they enter the sea after spawning (Sindermann, unpublished). *Saprolegnia* infections of Pacific salmon disappeared when the fish were placed in sea water (Earp *et al.*, 1953), although Vishniac and Nigrelli (1957) have suggested that brackish-water fishes may be parasitized by the Saprolegniaceae.

D. *Protozoa*

Sporozoa and Cnidospora* are among the best known and most serious pathogens of marine fishes, although representatives of other protozoan groups, such as the hemoflagellates and ciliates, have been studied (Laveran and Mesnil, 1902; Neumann, 1909; Tripathi, 1948; Brown, 1951; Laird, 1951; Reichenbach-Klinke, 1956d). Coccidia, Myxosporidea and Microsporidea have varied and often severe effects on their hosts, ranging from castration to nerve and muscle degeneration. Many of the species studied have characteristic and readily recognizable spore stages, which facilitate identification and encourage study. Most are specific for particular host tissues. For some, life cycles and transmission are adequately understood, but for many much remains to be learned, particularly about their ecology.

1. *Coccidia*

Severe and often fatal coccidian infections of mammals and birds have some counterparts in fresh-water fishes (Bespalyi, 1959) and to a lesser extent in marine species. A widely distributed disease of clupeoid fishes is that caused by *Eimeria sardinae* (Thélohan). The parasite localizes, often in massive numbers, in the testes (Fig. 4), where it may reduce reproductive capacity or cause complete sterility of the host (Pinto, 1956; Letaconnoux, 1960; Pinto and Barraca, 1961; Pinto *et al.*, 1961). *E. sardinae* has been reported from the sardine, *Sardina pilchardus* Walb., off Portugal (Pinto, *op. cit.*), the sprat, *Clupea*

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* An attempt has been made to conform to the revised system of classification of the Protozoa (Honigberg *et al* , 1964).

sprattus (L.) from the eastern North Atlantic (Thomson and Robertson, 1926), and the Atlantic herring, *Clupea harengus*, from the Baltic Sea (Dogiel, 1939; Dollfus, 1956), Barents Sea (Polyanski, 1955), White Sea (Shulman and Shulman-Albova, 1953), North Sea (Kabata, 1963), and the western North Atlantic (Sindermann, 1961a). It occurred in over 50% of sardines sampled by Pinto (*op. cit.*) and thus must be considered a significant limitation to the reproductive potential of that species.

Other coccidian parasites of the testes of marine clupeoids have been reported. Spores of *Eimeria brevoortiana* occur in the testes of menhaden, *Brevoortia tyrannus* (Latrobe), according to Hardcastle (1944) and spores of *E. nishin* have been described from Pacific herring by Fujita (1934). *E. brevoortiana* was found in 42% of 700 male fish examined, and was more common in adults than in juveniles. No spores were seen in females.

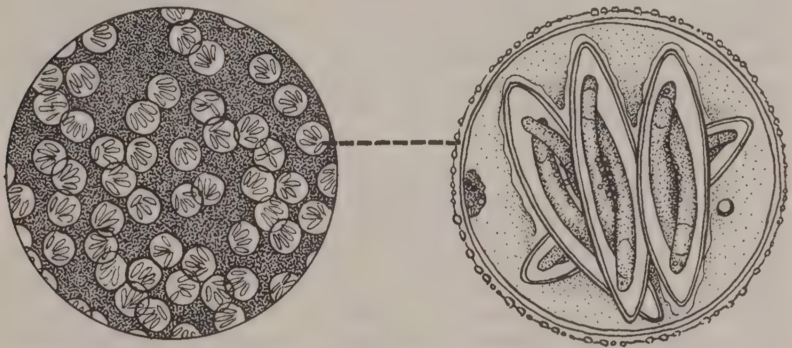

FIG. 4. Invasion of testes by *Eimeria sardinae* (right) and mature oöcyst (left). (Redrawn from Dogiel *et al.*, 1958, and Kabata, 1963.)

Eimeria may occur in other organs. *E. clupearum* (Thélohan) is found in the liver of clupeoids, often in abundance, but is usually not considered seriously pathogenic. *E. gadi* has been described as a pathogen of several gadoid species by Fiebiger (1913). It parasitizes the swimbladder, where *in situ* germination of spores can produce heavy infections. *E. anguillae* has been described as a parasite of the intestinal epithelium of eels in Europe (Léger and Hollande, 1922).

Members of another coccidian group, the Haemogregarinidae, have long been recognized as of widespread occurrence in blood cells of fishes. Although the parasites were first reported in 1901 by Laveran and Mesnil, the complete life history of marine members of the group is still unknown. Haemogregarines have been described from menhaden in Florida by Saunders (1964), from arctic char, *Salvelinus alpinus* (L.), in northern Canada by Laird (1961), from a mullet, *Mugil brasiliensis* Agassiz, in Brazil by Carini (1932), from javelinfish, *Coelorhynchus australis* (Richardson), in New Zealand by Laird (1952), and from many other fishes from diverse habitats (Laveran, 1906; Lebailly, 1906; Kudo, 1954). One species, *Haemogregarina bigemina* Laveran and Mesnil, has been reported from Europe, Canada, United States, South Africa, the Red Sea and the South Pacific (Laird, 1958; Saunders, 1960). The haemogregarines have not been reported as responsible for mortalities.

2. *Myxosporidea*

Diseases caused by Myxosporidea are common in marine as well as fresh-water fishes. The myxosporideans inhabiting organs such as the gall bladder are most frequently studied and described, but those localizing in the somatic muscles must be considered the most destructive and of greatest economic significance. Extensive necrosis of the flesh characterizes invasion of halibut, *Hippoglossus stenolepis* Schmidt, by two Myxosporidea: *Unicapsula muscularis* Davis which causes a condition known as " wormy " halibut, and *Chloromyxum* sp. which causes " mushy " halibut (Thompson, 1916; Davis, 1924). Both act to reduce the value of the fish as food. Muscle necrosis in swordfish, *Xiphias gladius* L., from Japan has been reported by Matsumoto (1954) to be caused by the myxosporidean *Chloromyxum musculoliquefaciens*, and a similar " jellied " condition of swordfish from the North Atlantic has been observed (McGonigle and Leim, 1937). Another cnidosporan, *Hexacapsula neothunni*, has been associated by Arai and Matsumoto (1953) with a jellied condition of yellowfin tuna, *Thunnus albacares* (Bonnaterre), from Japan, and Pérard (1928) has described the degeneration of muscles of mackerel, *Scomber scombrus* L., resulting from parasitization by *Chloromyxum histolyticum*.

" Milkiness "—a softening and liquefaction of the flesh of lemon sole, *Parophrys vetulus* Girard, and other species—was reported from the Canadian Pacific coast by Margolis (1953), Forrester (1956) and Patashnik and Groninger (1964) as due to a species of *Chloromyxum*. The condition known as " milkiness " in several species of fishes from the African coast has been associated with the presence of *Kudoa* (=*Chloromyxum*) *thyrsites* (Gilchrist). The parasite has been reported in snoek or barracouta, *Thyrsites atun* (Euphr.), by Gilchrist (1924); stockfish, *Merluccius capensis*, by Fletcher, Hodgkiss and Shewan (1951); and the John Dory, *Zeus faber* L., by Davies and Beyers (1947).

The same condition and parasite have been reported in *Thyrsites atun* from Australia by Johnston and Cleland (1910) and Willis (1949). " Milky " flesh deteriorates rapidly after the fish is caught, probably due in part to a proteolytic enzyme secreted by the parasite, as postulated by Willis. In South African waters, Davies and Beyers (*op. cit.*) found that three-fourths of the John Dory and stockfish were infected with *Kudoa thyrsites.* A quarter of all John Dory were too heavily infected to be suitable for filleting. The same parasite occurred in 5% of Australian barracouta (Roughley, 1951).

The flesh of clupeoid fishes is often parasitized by Myxosporidea which produce opaque white cysts and necrotic areas (Fig. 5). A *Chloromyxum* occurs in the pilchard, *Sardinops ocellata*, from South Africa (Rowan, 1956). Juvenile Atlantic herring, *Clupea harengus*, menhaden, *Brevoortia tyrannus*, and blueback herring, *Alosa aestivalis* (Mitchill) from the Atlantic coast of North America are often parasitized by *Kudoa* (=*Chloromyxum*) *clupeidae* (Hahn, 1918; Meglitsch, 1947; Sindermann, 1961b). Several authors (Tyzzer, 1900; Linton, 1901; Sindermann, 1957) have noted that the parasite occurred only in smaller and younger members of the host species. As many as 75% of 1-year-old Atlantic herring from certain parts of the U.S. (Maine) coast were parasitized, but adults were not infected. Linton speculated that there were fewer infections among older fish because the vitality of the diseased fish was so impaired that they fell victim to predators in larger proportional numbers than did healthy fish. It seems equally likely that invasion occurs early in the life of the host, that spores mature and escape from cyst areas, and that evidence of disease is absent by the time the host reaches maturity.

Among the anadromous fishes, the myxosporidean *Henneguya salminicola* Ward invades the flesh of several species of Pacific salmon, producing opaque white cysts described as " tapioca disease " (Fish, 1939). Spores of the parasite have also been seen in milky necrotic pockets in salmon from the eastern Pacific (Patashnik and Groninger, 1964). Similar pathological conditions and high prevalences have been described in salmon from the western Pacific by Akhmerov (1955).

It can be seen from even a brief review that muscle-inhabiting Myxosporidea are of world-wide distribution and economic significance. This is particularly true of members of the genus *Kudoa* which was created by Meglitsch (1947) to include species removed from the genus *Chloromyxum* that are histozoic with quadrate or stellate spores, These species are associated with necrosis of the flesh of living fish, and with rapid post-mortem deterioration and liquefaction.

The gall-bladder-inhabiting Myxosporidea, of which there are many

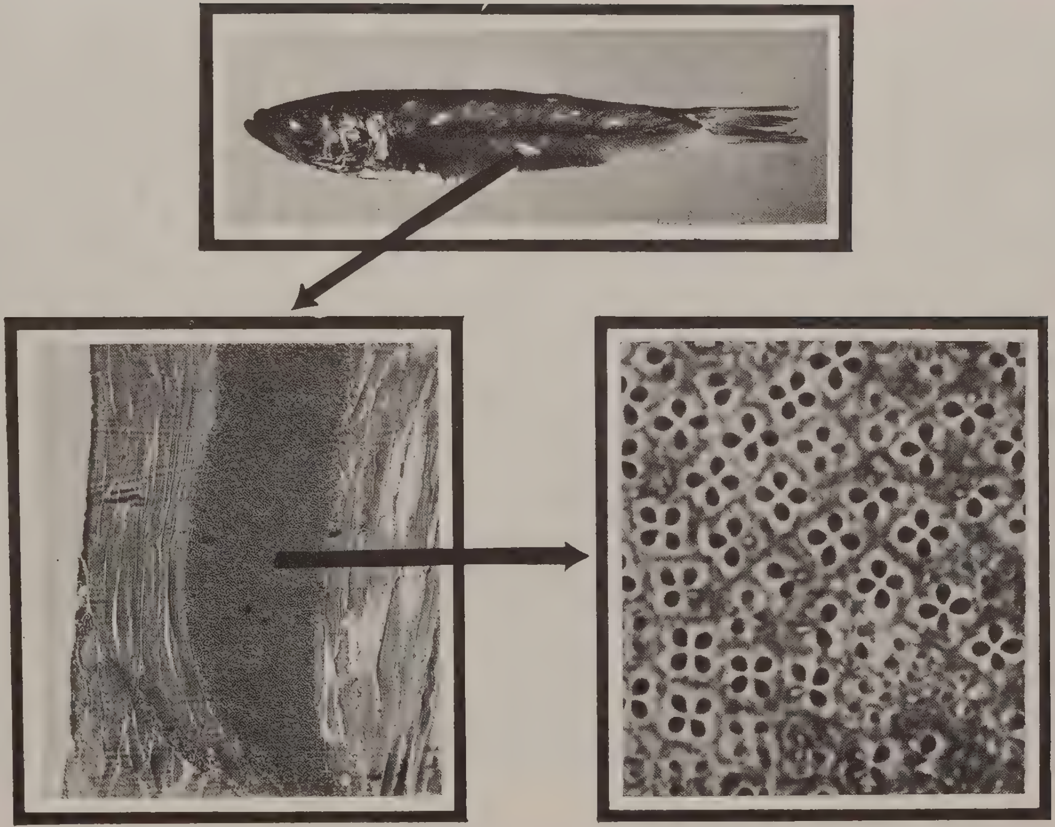

FIG. 5. *Kudoa clupeidae.* Gross appearance of cysts in flesh of herring (top), cyst in histological section (lower left), and individual spores (lower right).

species (Kudo, 1920), are of widespread occurrence in marine fishes. Heavy infections may cause enlargement, discoloration and disruption of function of the organ. Fantham and Porter (1912), who examined the widespread occurrence of gall bladder parasites in elasmobranchs and teleosts from the English and French coasts, found that myxosporidean parasitization caused inflammation of the organ, excess secretion of mucus and increase in viscosity of bile, enlarged livers and emaciation of the host.

Gill-invading Myxosporidea are not usually of serious consequence to marine fishes. However, Shulman (1957) described an epizootic of *Myxobolus exiguus* in the gills of mullet, *Mugil cephalus* (L.), from the Black Sea in which 500–600 kg of fish per kilometer were washed up on the western shore of the Crimean Peninsula during the spring of 1949. Mechanical disruption of gill function, caused by heavy infection with myxosporidean cysts, was considered the cause of death. No abnormalities were noted in the viscera.

Several species of Myxosporidea invade the cranial cartilages of fishes. One, *Myxobolus aeglefini* (Auerbach), occurs in plaice, *Pleuronectes platessa* (L.), hake, *Merluccius merluccius* (L.), and haddock, *Gadus aeglefinus* L., of the North Sea (Johnstone, 1906; Auerbach, 1906, 1912; Kabata, 1957b). Erosion and in some instances hypertrophy of head cartilage results. Effects of *M. aeglefini* do not seem as severe as those caused by *Myxosoma cerebralis* (Hofer) in salmonid fishes. *Myxosoma*, a highly infectious disease agent acquired early in life in fresh water, causes " whirling disease " of juvenile salmon and trout, as well as gross skeletal abnormalities (Bogdanova, 1960; Hoffman *et al.*, 1962). The disease has long been known in central Europe, and has recently been found in Russia and United States. Dannevig and Hansen (1952) have reported symptoms indicating *M. cerebralis* infections in very young herring reared in aquaria.

3. *Microsporidea*

Several serious diseases of marine fishes result from microsporidean invasion. Smelts, *Osmerus eperlanus*, from Europe (Weissenberg, 1911c) and *Osmerus mordax* from North America (Schrader, 1921; Fantham *et al.*, 1941) are often parasitized by *Glugea hertwigi* Weissenberg, which produces varying degrees of visceral involvement, to the extreme condition in which the body cavity is packed full of microsporidean cysts up to 9 mm in diameter. Heavy infections have been reported to prevent reproduction by mechanical occlusion of the vent (Haley, 1954; Sindermann, 1963) and lesser infections destroy areas of digestive tract and gonad and impair other metabolic functions. Haley found that 23% of the smelt he examined were infected; because of the serious pathological manifestations of the disease he suggested that it could be an important factor in the recently observed decline of the smelt fishery on the New Hampshire coast. Bogdanova (1957) reported that massive infections with *G. hertwigi* caused degenerative changes in sexual organs and death of the host. Dogiel *et al.* (1958) stated that infection of *O. eperlanus* caused functional disturbances in several organs, growth retardation, decline in fertility and mass mortality. Incidence of *Glugea* reached 25 to 50% and decline in stocks of *Osmerus* was attributed to the parasite (Annenkova-Khlopina, 1920). Templeman (1948) found a *Glugea*, probably *G. hertwigi*, in capelin, *Mallotus villosus* (Muller), spawning on the Newfoundland coast. Almost one-

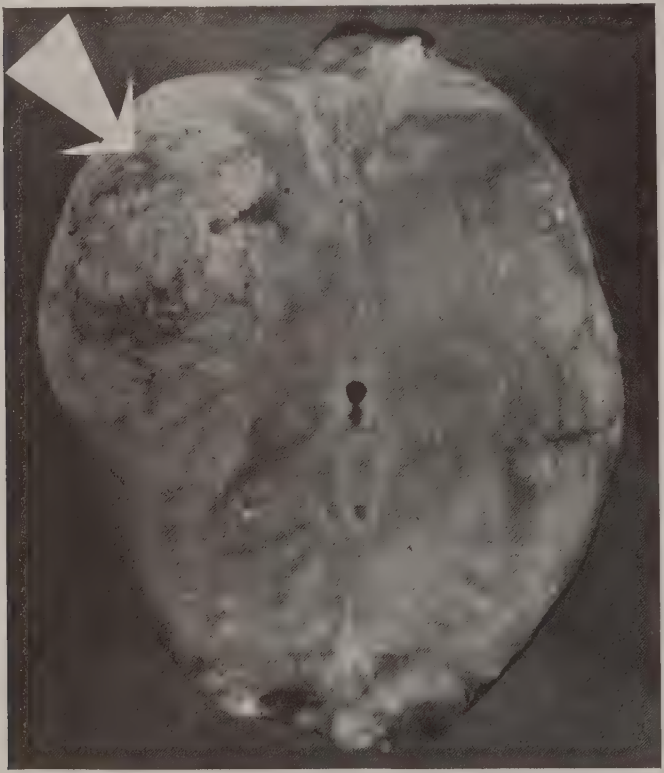

FIG. 6. Cross-section of *Macrozoarces americanus* through *Plistophora* cyst.

fourth of all fish examined carried cysts beneath the peritoneum or in the mesenteries.

Another species of the same genus, *G. anomala* (Moniez), was reported earlier (Weissenberg, 1913, 1921b) from European sticklebacks, *Gasterosteus aculeatus* L. and *Pungitius pungitius* (L.). Hypertrophy of connective-tissue cells, resulting in thick-walled cysts up to 4 mm in diameter, occurred externally and internally. Kudo (1924) and others described deformation of the host's body as a result of intensive *G. anomala* infection. The parasite has been reported as a cause of mass mortality in sticklebacks from the White Sea (Dogiel *et al.*, 1958).

Still another species, *Glugea punctifera* Thélohan, is a serious intramuscular parasite of mintai, *Theragra chalcogramma*, from the Okhotsk and Japan Seas (Akhmerov, 1951). Cod from the Okhotsk Sea were also infected with this *Glugea.*

The microsporidean *Nosema lophii* (Doflein) produces large tumor-like cysts in the central nervous system of the goosefish or angler-fish, *Lophius piscatorius* L. Parasitization results in extensive hypertrophy of host ganglion cells as the cyst develops, producing dark grape-like enlargements on the nerves. Weissenberg (1909, 1911a, 1911b, 1911c) found abundant infections at Naples; the parasite has also been reported from England and France.

Another microsporidean, *Plistophora macrozoarcidis* Nigrelli, is an important parasite of the ocean pout, *Macrozoarces americanus* (Bloch and Schneider). Extensive tumor-like intramuscular cysts, often several centimeters in diameter (Fig. 6), seriously reduce the marketability and utilization of this fish in the United States. Appearance of fillets containing parasite cysts on the market during 1943–44 was responsible in part for curtailment of a developing fishery for *Macrozoarces*, and in a few years led to complete disappearance of the species as a food fish in the United States (Fischthal, 1944; Sandholzer *et al.*, 1945). Recent interest in reviving the fishery seems contingent on development of a suitable method of eliminating parasitized fish from processing procedures.

Plistophora cysts can often be recognized by conspicuous bulges on the body of the host. The lesions are usually exposed during filleting, and a pus-like exudate of spores and tissue debris occurs when such areas are cut. Life cycle stages have been described by Nigrelli (1946). No ulceration has been seen, so the method of spore liberation has been postulated as death and decay of the host. The massive involvement of individual fish suggests sporulation *in situ.* Repeated auto-infection is possible in some species of Microsporidea, according to Kudo (1954), and some suggestion of it was found in *Macrozoarces*, since many specimens were characterized by immense numbers of minute infections involving single muscle fibers (Olsen and Merriman, 1946).

Other species of *Plistophora* invade the flesh of fish also. Body muscles overlying the visceral cavity of the long rough dab, *Drepanopsetta hippoglossoides* Gill, are invaded by *P. hippoglossoideos* Bosanquet, forming cysts up to 10 mm long. Kabata (1959) found the parasite to be widely distributed in the North Sea. Cod of the Barents Sea were found to be infected with *P. gadi* by Polyanski (1955). The parasite produced large tumors (5 to 8 mm) in the body muscles.

III. Other Parasitic Diseases

The invasive diseases, as considered in this paper, include those caused by the larger parasites—those that are non-multiplicative in the fish host once invasion has occurred. Of primary concern in marine fishes are the various parasitic worms and the tissue-invading copepods. Omitted from this discussion are leeches, most ectoparasitic copepods, parasitic Cirripedia and Isopoda, and lampreys, which, although of occasional concern, probably do not often exert serious effects on marine fish populations. Since the worms and copepods are large, conspicuous and often abundant, they have been observed and studied extensively.

A. *Helminths*

The helminths—trematodes, cestodes, nematodes and acanthocephala—are common parasites of marine fishes. Usually it is as larvae that the worms are of greatest significance. Adults occur in the digestive tract, but larvae are usually found in the flesh or in the viscera. The effects of worm larvae on the host include growth retardation, tissue disruption, metabolic disturbances, and even death in heavy infestations. Added economic effects include discarding of otherwise edible fish products, delay in processing operations and loss in oil yields.

1. *Trematodes*

Adult digenetic trematodes are common in the digestive tracts of marine fishes. Yamaguti (1958) recognized 367 genera and 1390 species from fish, but it is as larvae—as migrating cercariae and as metacercariae—that trematodes seem to be of greatest significance to the fish host. Marine teleosts serve as intermediate hosts for many trematodes, particularly those whose definitive hosts are shore-inhabiting or fish-eating birds and mammals. Metacercariae of such worms encyst beneath the skin or in the body of inshore fishes. An excellent example is the trematode *Cryptocotyle lingua* (Creplin), whose life cycle in the western North Atlantic (Fig. 7) involves the periwinkle, *Littorina littorea* (L.), the Atlantic herring, and the gull, *Larus argentatus* Pontoppidan. Originally a parasite of comparable species in northwestern Europe (Christensen and Roth, 1949), the parasite was introduced in North American waters near the middle of the nineteenth century, probably with its snail host (Stunkard, 1930). Cercariae of *Cryptocotyle* invade and encyst in the fins and integument of herring and a number of other inshore western Atlantic species, causing the formation of conspicuous pigmented cysts or " black spots ". It has

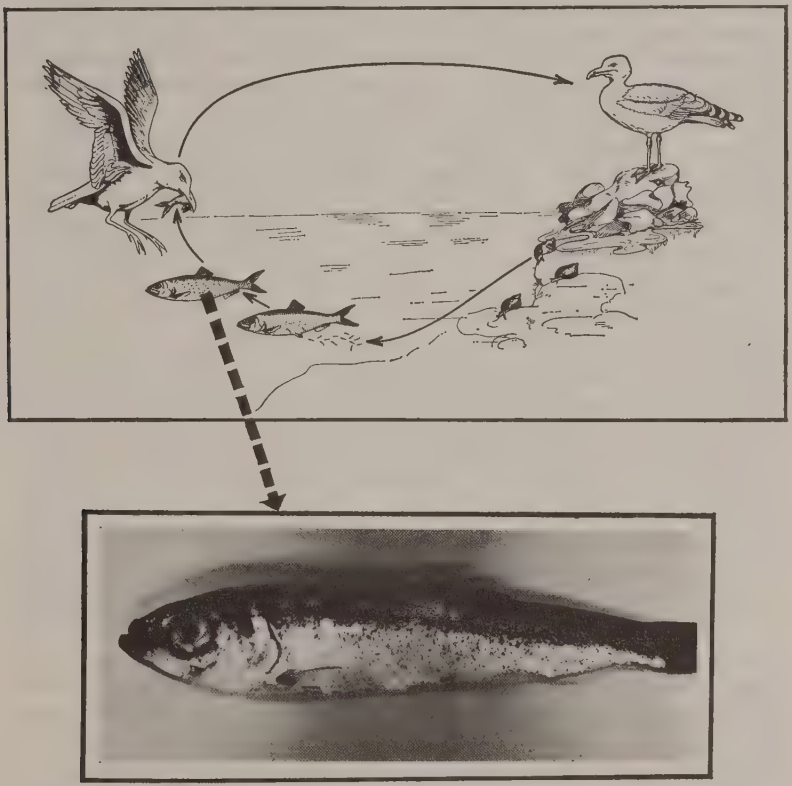

FIG. 7. Life cycle of *Cryptocotyle lingua* in the western North Atlantic (above) and results of parasitization of Atlantic herring (below).

been demonstrated experimentally (Sindermann and Rosenfield, 1954b) that massive cercarial invasion will blind and kill immature herring, and it has been postulated that invasions of comparable magnitude are possible in the inshore habitat of the fish.

Another larval fluke, *Stephanostomum baccatum* (Nicoll), occurs in a number of marine fishes, particularly flatfishes, from the Canadian Atlantic coast to the Baltic Sea. The life cycle, as elucidated by Wolfgang (1954), involves gastropods of the family Buccinidae, the winter flounder and other pleuronectids, and the sea raven, *Hemitripterus americanus* (Gmelin). Metacercariae occur in unpigmented cysts, concentrated on the blind side of the flatfish and in the fins, often in great numbers in larger fish. The parasite was originally reported from a halibut from the English coast by Nicoll (1907) and was later found in American plaice, *Hippoglossoides platessoides* (Fabr.), by Nicoll (1910). Dawes (1947) recorded six species of European flatfish as hosts.

Many other larval trematodes occur in marine fishes. Bykhovskaya-Pavlovskaya and Petrushevskii (1959), for example, have listed 46 species of metacercariae from the USSR, of which almost half occurred in marine or estuarine species. Fish-eating birds and mammals have been identified as definitive hosts of most of these parasites. Mass mortalities due to larval trematode invasion have been reported from the Aral and Caspian Seas (Dogiel and Bykhovskii, 1934; Dubinin, 1949). Red mullets, *Mullus barbatus* (L.) and *M. surmuletus* (L.) in the Mediterranean Sea are often parasitized by larval trematodes, according to Orlandini (1957).

Adult digenetic trematodes are common parasites of the digestive tract, but are usually not a cause of serious disease. Cosmopolitan fish species harbor a number of adult trematodes throughout their range. Manter (1955) has reviewed the zoogeography of many, including the 20 species from Atlantic eels. He found that most of these trematodes were of marine origin, and that those characteristic of the eel in Europe were different from those reported in America. Apparently the parasites were acquired after the larval eels had separated in the Atlantic. Many of the trematode species found in marine fishes of a given geographic region are peculiar to that region, although similarities of fauna from major ocean areas such as European Atlantic and Mediterranean exist.

Among the monogenetic trematodes parasitic on gills and body surfaces of marine fishes, a number become serious parasites in aquaria, where conditions for reinfestation are optimum. Only rarely, and under unusual conditions, have members of this group been demonstrated to be pathogenic to fish in natural habitats. Heavy infestation of sticklebacks in the White Sea was felt to be partially responsible for mass mortalities (Dogiel *et al.*, 1958). Fish had been isolated in tide pools, and the trematodes multiplied to numbers up to 1000 per fish. Two parasite species, *Gyrodactylus arcuatus* Bychowsky and *G. bychowskyi* Sproston, were involved; most of the fish died. Dogiel and Lutta (1937) studied an epizootic in the Aral Sea sturgeon, *Acipenser nudiventris* Lov., caused by the gill trematode *Nitzschia sturionis* (Abilgaard). As a result of mortalities during 1936 the fishery, which previously had reached a peak of 400 tons per year, ceased to be of commercial significance for the next 20 years (Osmanov, 1959). Recent level of infestation in all conditions of salinity was reported at 50 to 75%.

2. *Cestodes*

Adult cestodes are common and occasionally harmful digestive-tract parasites of fishes, but, as with the trematodes, larval stages are of greatest concern to man. Larval tapeworms occur frequently in the viscera and flesh of marine and estuarine fishes (Fig. 8). The definitive hosts of many of these parasites are elasmobranchs or fish-eating birds and mammals. Tapeworms which localize in the body muscles may occur in large numbers in individual hosts. Linton (1907) described such an infestation in butterfish, *Poronotus triacanthus* (Peck), of the North American east coast, in which several thousand larvae could be found in individual fish. Encysted plerocercoids, less than a millimeter in diameter, were concentrated in the flesh adjacent to the vertebral column, and up to 75% of individuals in a sample were heavily infected. The parasite was identified as *Otobothrium crenacolle* Linton, which matures in the spiral valve of certain shark species, particularly the hammerhead, *Sphyrna zygaena* (L.). Ripe, highly motile proglottids of the tapeworm are shed in the feces and presumably ingested by butterfish and other teleosts, in which the embryos invade the musculature and encyst.

Other members of the cestode order Trypanorhyncha occur as adults in the digestive tract of elasmobranchs, and as larvae in the flesh and viscera of many teleost species. Elongate larvae of *Poecilancistrium robustum* (Chandler), called "spaghetti worms", are very abundant in the flesh of drum, *Pogonius cromis* (L.), in the Gulf of Mexico. According to Chandler (1954) some municipal health departments have considered banning drum from markets because of frequent worm parasitization. Oppenheimer (1962) reported that spaghetti worms were common in the flesh of many other fishes from the Gulf of

Mexico. Large spotted seatrout, *Cynoscion nebulosus* (Cuvier), harbored up to 100 larval worms, and as much as 44% of a sample were infested (Chandler, 1935a, 1935b). Many food fishes, such as herring, hake and mackerel, have been reported to harbor other trypanorhynch larvae (Johnstone, 1912b; Linton, 1923; Ruszkowski, 1934; Kahl, 1937; Young, 1955; Rae, 1958). As an example, *Grillotia erinaceus* (van Beneden) is so common in many North Atlantic teleosts that an extensive literature on its occurrence existed in the nineteenth century. Pleroceroids of the cestode were described by Johnstone (1912b) as among the most abundant helminth parasites of Irish Sea fish; they occurred usually in mesenteries or the stomach wall, but, in hake and halibut, in the flesh adjacent to the vertebral column. The life cycle was elucidated by Ruszkowski (1934). Rae (1958), in a study of the cestode in halibut of the eastern North Atlantic, found heaviest infestations in larger fish; 10 to 20% of catches from banks off the west coasts of Scotland and Ireland were infested. Wardle (1932, 1935) reported the worm from the Canadian Pacific coast. Linton (1925) described the adult stages of this and other Trypanorhyncha from sharks and skates, and Dollfus (1942) has made an excellent critical examination of this interesting tapeworm group. Kändler (cited by

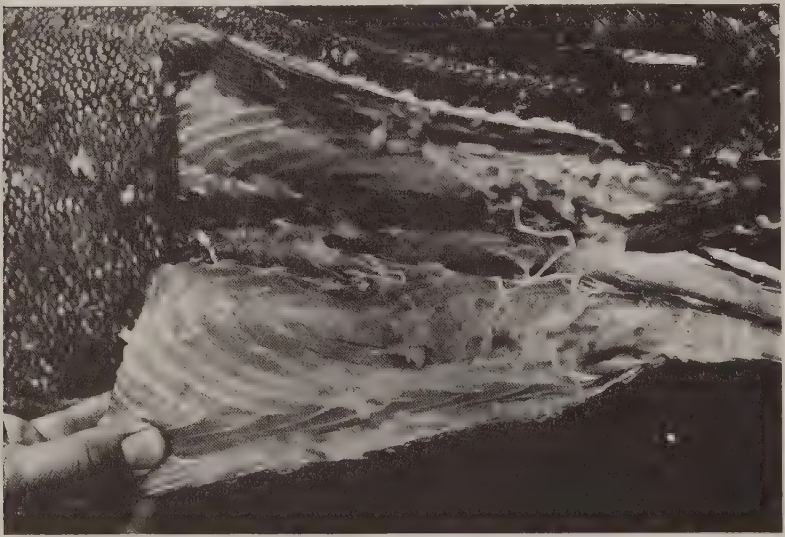

FIG. 8. Larval tapeworms in the flesh of a rudderfish, *Seriola zonata* (Mitchill).

Mann, 1954) reported disruption of growth as a result of tapeworm infestation of Baltic Sea turbot, *Rhombus maximus* (L.). Fish in their second year of life were most seriously parasitized and complete recovery of normal growth rate took several years.

Adult cestodes may occur in significant numbers in the digestive tract of fishes, although their prevalence in marine teleosts is low in comparison with that of other helminths. Linton (1941) described many representatives from the western North Atlantic, and Wardle (1932, 1935) surveyed the Pacific coast fauna. The Pseudophyllidean genus *Eubothrium* Bloch (*Abothrium* Lühe) is common in marine and fresh-water fishes. Several species occur in the digestive tracts of cod, haddock, herring and other sea fishes (Nybelin, 1922; Sprehn, 1934). Many other representatives of the Pseudophyllidea occur in teleost fishes (Wardle and McLeod, 1952), while the order Tetraphyllidea is well represented among the elasmobranchs (Woodland, 1927; Baer, 1948; Williams, 1958).

3. *Nematodes*

The nematode parasites of marine fishes have received attention primarily because certain larvae that infest the flesh and viscera reduce the commercial value of the host. An outstanding example is the codworm, *Porrocaecum decipiens* (Krabbe). The definitive host is the harbor seal, *Phoca vitulina* L., according to Scott (1953), and larvae occur in the flesh of cod, smelt, plaice, ocean pout and other species of inshore marine fish (Heller, 1949; Scott, 1950, 1954, 1955). Larvae may also pass from fish to fish if infected smaller individuals (for example smelt) are eaten by cod. Olsen and Merriman (1946) reported ocean pout from New Brunswick to be heavily infested—to the extent that the flesh of some fish had a porous appearance. A similar parasitization of ocean pout had been described from the same area 25 years previously (Clemens and Clemens, 1921). Scott and Martin (1957, 1959) found high prevalence but geographic variations in infestation of cod from the Canadian Atlantic coast; infestation decreased in deeper waters and increased with age of the host. A survey of *Porrocaecum* adults in seals (Scott and Fisher, 1958) did not disclosed a direct distribution relationship with larvae in cod.

Templeman *et al.* (1957), in an extensive survey of groundfish in the Newfoundland fishing area, found larval *Porrocaecum* in cod, smelt, plaice, witch flounder (*Glyptocephalus cynoglossus* (L.)), haddock and redfish (*Sebastes marinus* L.). Examination of over 15 000 fish disclosed that over three-fourths of all larval nematodes were *Porrocaecum*; the remainder were other larval Anisakinae. Fishes such as halibut, pollock

(*Pollachius virens* (L.)) and sea raven (*Hemitripterus americanus* (Gmelin)) living in the neighborhood of seal colonies were infested also. Marketing problems with worm-infested fillets were felt to be more serious with *Porrocaecum*, whose larvae are large and brown-colored, than with other larval Anisakinae, which are small and white.

Studies of larval marine nematodes of the sub-family Anisakinae by a number of authors (Kahl, 1938a; Baylis, 1944) lead to some confusion about identification of larval *Porrocaecum*, since small specimens may lack the diagnostic intestinal caecum which separates this genus from others. Feeding studies with seals (Scott, 1953, 1956) established that most larval worms from cod, plaice, smelt and eelpout of the western North Atlantic were actually *P. decipiens*. Other nematode genera represented by larvae in food fishes of the North Atlantic include *Eustoma* and *Anasakis*. Templeman *et al.* (1957) have summarized the problems inherent in specific identification of larval Heterocheilidae.

Porrocaecum larvae have been reported from 18 species of Pacific fishes, including the Pacific cod, *Gadus macrocephalus* Tilesius, by Yamaguti (1935). Smelt, cod, redfish and other species from the North Sea were also found to harbor this nematode (Martin, 1921; Kahl, 1936, 1939). Grainger (1959) identified as *Porrocaecum* larval nematodes from cod and other fishes from Greenland waters and the Barents Sea.

Infestation of cod livers by larval *Contracaecum aduncum* (Rud.), also of the subfamily Anisakinae, has been responsible for considerable economic losses in the Baltic Sea, according to Markowski (1937), Shulman (1948, 1959), Petrushevskii and Shulman (1955) and Getsevichyute (1955). Numbers of worms per liver reached 100, and parasitized fish suffered loss of total weight and liver mass (Fig. 9). Larger, deeply penetrating worms were more harmful, and young fish or spawning fish showed less tolerance to infestation. Liver fat content and oil yield were seriously reduced by parasitization. *Contracaecum* was also found in cod from the White and Murman Seas, but in lesser frequencies.

An interesting example of nematode parasitization that is of serious consequence to the host has been described by Janiszewska (1939). Flounders of the eastern Atlantic are often heavily parasitized by *Cucullanellus minutus* (Rud.). Larvae invade the intestinal wall, causing extensive pathological changes. After overwintering, the worms re-enter the lumen of the digestive tract and mature during early summer.

A common larval nematode of the subfamily Acanthocheilinae is *Eustoma* (*Anacanthocheilus*) *rotundatum* (Rud.), which occurs as a larva in the mesenteries and viscera of many North Atlantic fishes, including cod, haddock, redfish, flatfishes and herring (Kahl, 1938b). The larvae may occasionally invade the flesh, particularly after the host fish is killed. Several recent papers from The Netherlands (Kuipers *et al.*, 1960; Roskam, 1960; van Thiel *et al.*, 1960) described severe human digestive disturbances after eating lightly salted " green " herring that contained larval *E. rotundatum*. As with other larval Heterocheilidae, the taxonomy of the parasite is still confused; Punt (1941), Berland (1961) and Roskam (1963) considered it a member of the genus *Anisakis*.

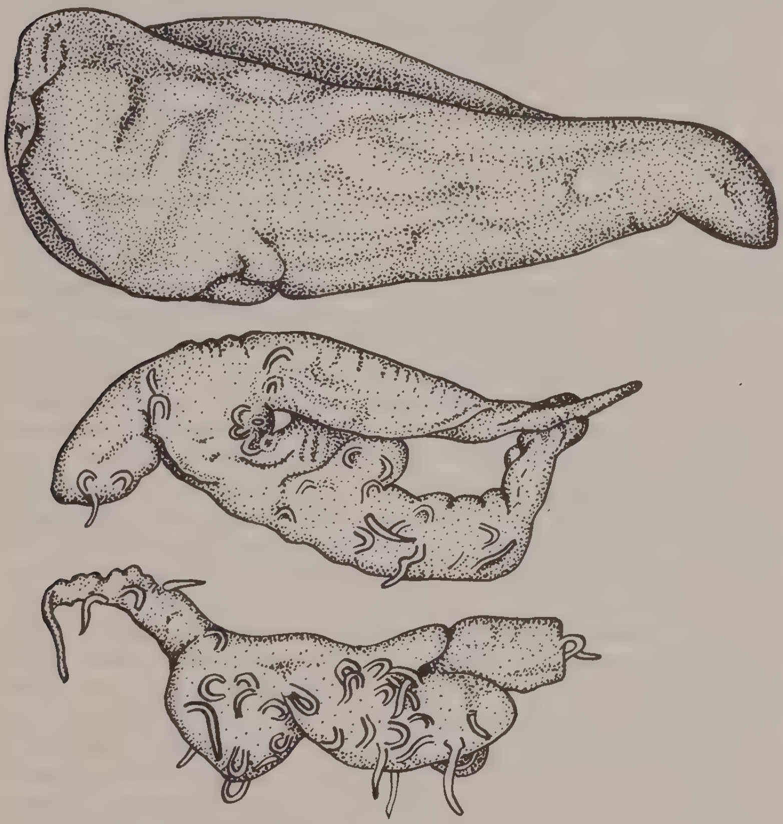

Fig. 9. Pathological livers resulting from infestation by larval *Contracaecum*. Livers are from Baltic cod of equal size, and the uppermost is normal. (Redrawn from Dogiel, Petrushevskii and Polyanski, 1958.)

It can be seen readily from these brief examples that infestation of marine fishes by larval nematodes is a matter of serious concern in many parts of the world. Adult nematodes, inhabitants of the digestive tract, occur in many species of marine fish, but appear to do less damage to the host. Among those that might be mentioned, *Camellanus melanocephalus* (Rud.) occurs in the stomach and pyloric caeca of tuna and mackerel, and *Proleptus obtusus* Duj. occurs in sharks.

4. *Acanthocephala*

The " spiny headed " worms are represented as adults and as larvae in marine fishes. A common parasite of North Atlantic species is the acanthocephalan *Echinorhynchus gadi* Müller. It has been reported (Linton, 1933) from the digestive tract of 54 fish species in the Woods Hole region. The worm occurs in *Macrozoarces americanus* in the western North Atlantic (Nigrelli, 1946) and in *Zoarces viviparus* (L.) from the English coast (Nicoll, 1907) and the Baltic (Markowski, 1939). It is circumpolar in distribution; having been found in diverse teleosts from northwestern Canada, Bering Sea, Kamchatka Peninsula and Japan, as well as from the Baltic Sea, White Sea, Murman coast, North Sea and Gulf of Maine (Dollfus, 1953). Another common acanthocephalan from the North American coast is *Telosentis tenuicornis* (Linton), found in a wide range of marine fish, including spot, *Leiostomus xanthurus* Lacépède (Huizinga and Haley, 1962), Atlantic croaker, *Micropogon undulatus*, and Atlantic threadfin, *Polydactylus octonemus* (Girard) (Chandler, 1935b) and the sand seatrout, *Cynoscion arenarus* Ginsburg, and pigfish, *Orthopristis chrysopterus* (L.) (Bullock, 1957).

Pomphorhynchus laevis (Müller) is a common parasite of many European marine fishes, including gadoids, flatfishes and eels. It may occur in great numbers in the gut or it may penetrate the gut wall and encyst in the viscera (Wurmbach, 1937; Shulman, 1959).

Larval acanthocephala are common in the viscera of many marine teleosts but have not been reported in the epizootic proportions occasionally seen in fresh water—for example, several species, including *Corynosoma semerme* (Forssell), *Corynosoma strumosum* (Rud.) and *Bolbosoma vasculosum* (Rud.) occur as adults in fish-eating birds and mammals, and as larvae in mesenteries and viscera of many species of sea fishes.

B. *Parasitic copepods*

Marine fishes are parasitized by a variety of copepods, of which several members of the families Lernaeoceridae, Pennellidae and Sphyriidae are particularly injurious to the host. Usually the adult females become highly modified and penetrate the flesh, often causing extensive ulceration.

Lernaeocera branchialis (L.) is a parasite of the gill region of gadoid fishes, particularly cod, whiting, pollock and other species from both sides of the North Atlantic and from the Pacific (Dollfus, 1953; Shulman and Shulman-Albova, 1953; Kabata, 1961; Sherman and Wise, 1961; and others). *L. branchialis* has been described as a heart parasite by Schuurmans-Stekhoven (1936) and Schuurmans-Stekhoven and Punt (1937) since the anterior end sometimes penetrates the bulbus arteriosus of the host. It has been the object of numerous studies, was reported in the scientific literature as early as 1762 by Strøm, and is considered one of the most harmful of the copepods parasitic on marine fishes. Intermediate hosts of the parasite include the lumpfish, *Cyclopterus lumpus*, flounder, *Pleuronectes flesus*, and several other pleuronectids. The adult female copepods, usually numbering one to three but occasionally more, attach to the gill region of gadoids. The head penetrates sometimes to the heart, in other cases to the ventral aorta or branchial arteries, causing connective-tissue hypertrophy and the formation of blood-filled lacunae. Invasion of the heart causes thickening of the walls so that the lumen of the organ is markedly reduced (Mann, 1954). Affected fish are almost always below average weight, and death of young cod can result from blood loss and pathological changes in heart and aorta. Mann (1952) reported that infested cod were 20 to 30% underweight, and had a lower erythrocyte count and decreased hemoglobin content of the blood. Extreme emaciation of whiting, *Gadus merlangus* L., was reported by Scott (1929) as the result of *L. branchialis* infestation. A second species, *L. obtusata*, has recently been distinguished by Kabata (1957a) as a parasite of the haddock. Separation was based on minor morphological variations in the adult females, site of penetration and characteristics of the male. Severe impairment of infested haddock, in the form of anemia, loss of weight, loss of liver fat and possible retardation of sexual development, was noted (Kabata, 1958). Walford (1958) cited results of a 2-year sampling in one English fishing port which disclosed *Lernaeocera* parasitization of 10% of haddock, 80% of whiting and 20% of cod. Parasitized fish were as much as 23% below normal weight.

A second well-known tissue-invading copepod is *Sphyrion lumpi* (Krøyer), widely distributed in the North Atlantic on the redfish and several other species (Fig. 10). It has been reported from the Norwegian coast (Lüling, 1951), West Greenland and the Norwegian Sea (Hansen, 1923), Newfoundland (Templeman and Squires, 1960), and the Gulf of Maine (Herrington *et al.*, 1939; Nigrelli and Firth, 1939; Sindermann, 1961c). In the western North Atlantic *Sphyrion* is primarily a parasite of redfish, but to the eastward—Iceland and northwestern Europe—lumpfish and wolffish are more likely to be hosts. The parasite penetrates deep in the flesh where extensive host connective-tissue encapsulation occurs around the anchor-like brown anterior extensions of the body. External ulcerations are also common. After death of the parasite the " cysts " persist as unsightly masses in the flesh for a number of years. These cysts must be removed from fillets before marketing. An interesting and still unsolved aspect of *Sphyrion* infestation of redfish is its marked geographic variation in occurrence; major centers of abundance are in the Gulf of Maine and off the coast of Labrador, and minor centers are on the southeast part of the Grand Bank and in the southern Gulf of Saint Lawrence. The parasite is absent from other major fishing banks of the western North Atlantic. According to Mann (1954) the extent of attacks on haddock varies

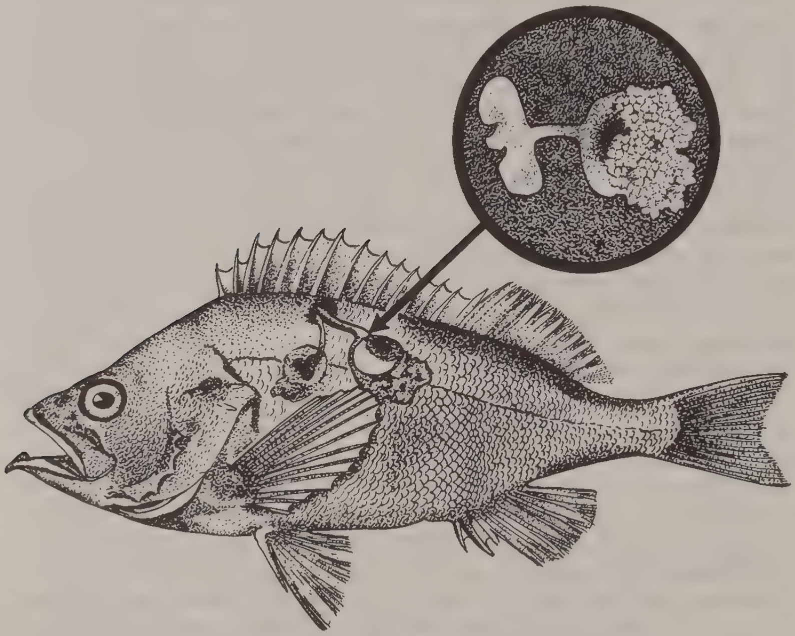

FIG. 10. The tissue-invading copepod *Sphyrion lumpi* in a redfish and removed to show anterior anchor.

with the fishing ground, and heaviest infestations are off the North American coast, where up to 10% of fish carry the parasite.

Another interesting parasitic copepod is *Lernaeenicus sprattae* (Sowerby) which occurs embedded in the eye or occasionally in the dorsal body muscles of sprat and sardines in Europe (Baudouin, 1904, 1905; Wilson, 1917). According to Baudouin, the parasite is called " pavillon " by sardine fishermen, because it has three distinct body parts, showing the three colors of the French tricolor, called " pavillon " by sailors. The long thin body and egg cases of the parasite trail posteriorly as the host swims.

Among the largest of the tissue-invading copepods are members of the genus *Pennella*. *P. exocoeti* (Holten) from flying fish, *Parexocoetus brachypterus* (Richardson), and *Pennella filosa* (L.) from swordfish and ocean sunfish, *Mola mola* (L.), may reach a length of 20 cm. The adult female of this and other members of the genus may be found almost anywhere on the host's body, with the head and neck embedded in the host organs, where large hard cysts are formed (Gnanamuthu, 1957).

Parasitic copepods other than the tissue-invading forms may occasionally damage marine fish. Surface abrasions and lesions caused by the parasites can be of serious consequence to the fish host directly or as a route of entry for secondary invaders. Salmonids in the North Pacific and the North Atlantic are often parasitized by *Lepeophtheirus salmonis* (Krøyer), an ectoparasite which causes severe skin erosion, and may even kill the fish host in heavy infestations (White, 1940, 1942; Margolis, 1958). Several members of the lernaeopodid genus *Clavella*, parasitic on the fins and in the branchial and buccal cavities of gadoid fishes, may cause lesions and tumors (Poulsen, 1939; Nunes-Ruivo, 1957; Kabata, 1960, 1963c). Lüling (1953) has described an instance of tissue damage in tuna, *Thunnus thynnus* (L.), caused by the caligid *Elytrophora brachyptera*.

IV. Genetic and Environmentally Induced Abnormalities

In addition to abnormalities which can be associated with particular disease-causing organisms, marine fishes offer numerous examples of physiological or structural defects, or conditions which may have genetic or other causes. A number of inherited abnormalities of fishes have been studied, including defective spinal columns, pigmented tumors, cataracts, kidney tumors and association of certain pigment-producing genes with physiological disturbances (Gordon, 1954). On the basis of his review, Gordon felt that abundant evidence existed for genetic control of certain diseases and abnormalities of fishes, despite the fact that the hereditary factors involved were usually complex.

Probably the most thorough studies have been made of the genetics of pigmented tumors (Gordon, 1948, 1950). Neoplastic growths in which pigmented cells play a dominant role are found in many animals, and such neoplasms can be among the most malignant tumors known. Among fishes, neoplasms developing from melanophores are the commonest type of pigment-cell tumor, whereas tumors arising from other chromatophores are rare. For example, Gordon (1948) found melanotic tumors in marine or fresh-water representatives of 11 orders of elasmobranchs and teleosts. Takahashi (1929, 1934) in a 13-year survey of many types of tumors in 100 000 fish from the Sea of Japan found three melanomas, one guanophoroma and one allophoroma. Schmey (1911) reported a xanthoma from a single European shark and Smith (1934) an erythrophoroma in an American winter flounder.

Epidermoid carcinomas have been reported from several species of marine fishes. Johnstone (1924a) reported an instance in whiting, Williams (1929) a case in pollock, and Beatti (1916) several examples in drum. Odontomas have been reported in a croaker, *Micopogon opercularis*, from South America (Roffo, 1925), and a haddock from the Grand Bank (Thomas, 1926). Mesenchymal tumors have been found in cod by Johnstone (1920, 1924b, 1926) and Williams (*op. cit.*). Osteomas of the vertebrae were observed frequently in the red tai, *Pagrosomus major*, a Japanese food fish, by Takahashi (1929). Nerve-sheath tumors (neurilemmomas) are frequent in the snappers (Lutianidae). Lucké (1942) estimated that up to 1% of the snappers found in Tortugas waters had such tumors, and were called " cancer fish " by fishermen. Thomas (1931), Schlumberger and Lucké (1948), and Lucké and Schlumberger (1949) thoroughly reviewed the literature on tumors in fishes and found that more than 120 species were involved. On the basis of their review, the authors concluded that all the major varieties of tumors that occur in mammals and birds occur in cold-blooded vertebrates.

Goiter (thyroid hyperplasia) has been reported frequently from fresh-water hatcheries (see, for example, Gaylord and Marsh, 1914), but occurs only rarely in marine fishes held in aquaria. Schlumberger (1955) observed goiter in a number of pilotfish, *Echeneis naucrates* L., held in the Philadelphia Aquarium for long periods. Other species held in the same low-iodine water did not develop goiter, suggesting species variability in metabolic need for iodine. Schlumberger observed that the few reported examples of thyroid tumors in marine fishes usually occurred in those kept in aquaria for long periods. Such tumors were especially characteristic of pilotfish and developed within a year after introduction of normal fish. Nigrelli (1952b) reported malignant thyroid tumors in both wild and captive marine fish.

Tumors and hyperplastic growths in fishes may have a number of causes other than genetic. Viral etiology for diseases such as lymphocystis has already been considered. Kudo (1924) and Nigrelli and Smith (1938, 1940) found Microsporidea and Myxosporidea associated with tissue hyperplasia in certain fishes. Smith (1935) reported papillomas of flounders possibly associated with invasion of larval trematodes, and Reichenbach-Klinke (1955b) cited several instances of fungi associated with tumors.

Increasing levels of pollution in the marine environment, in addition to killing fish and destroying habitats, may produce abnormalities. In an interesting comparison of marine fishes taken in polluted and unpolluted areas, Young (1964) described changes in consistency of flesh, reduced weight, external lesions, exophthalmia and papillomas as characteristic of fishes from grossly polluted waters off California. External lesions on killifish, similar to those found on trawled species, were produced experimentally by introducing sewer effluent diluted with sea water. The possible association of pollution with increased occurrence of neoplasms in fishes had been made previously. Lucké and Schlumberger (1941) noted the common occurrence of epitheliomas in catfish, *Ictalurus nebulosus* (LeSueur), from the Delaware River, and Russell and Kotin (1957) reported on papillomas of white croakers, *Genyonemus lineatus* (Ayres), from the same California area studied by Young.

Abnormalities other than tumors have long attracted scientific attention also. An unusual condition described as "jellied" flesh, noted in several flatfish species, seems unrelated to a disease organism. Templeman and Andrews (1956) reported the condition in 40% of the catch of large American plaice, *Hippoglossoides platessoides* (Fabr.), fished in cold waters of the Grand Bank of Newfoundland. Higher water content and lower protein content made fillets perpared from affected fish unsuitable for market. Most of the fish above 60 cm were jellied. The authors postulated that large fish in cold waters could not adequately meet protein demands of gonad development, tissue maintenance and growth. Evidence was cited for similar conditions in other flatfish species as well as in cod and haddock that suggested a generalized condition of muscle-protein impoverishment under stresses of age, low temperature and gonad development.

Abnormalities in morphology are abundantly described in the scientific literature. Gemmill (1912) published a book on teratology of fishes and Dawson (1964) has compiled a bibliography of fish anomalies which contains over a thousand references. Structural abnormalities in several skate species have been described recently by Templeman (1965). Included were such conditions as: separation of pectoral fins from the head, which has been observed repeatedly in the past in other parts of the North Atlantic; curvature of the vertebral column, a condition found in many teleosts also; and " blunt snout ", caused by skeletal defects. Letaconnoux (1949), who reported on teratological studies of marine fishes landed in France, also noted malformations of the pectoral fins in skates, and described an interesting condition of pigmentation of the normally unpigmented blind side of plaice, often associated with incomplete eye migration. Letaconnoux also observed a common abnormality of " short tail "—a definite abbreviation of the caudal region seen in many species of fishes, due to twisting, compression or fusion of vertebrae. A similar shortening, torsion and diminution of the caudal region has been observed frequently in immature Atlantic herring from the Gulf of Maine, especially in samples taken by bottom trawls rather than conventional surface gear (Sindermann, unpublished). Individuals of other species, such as haddock, have also been found with spinal abnormalities in the western North Atlantic. Although this condition may be due to a bone disease, it seems more likely that these and other structural abnormalities can be attributed to defective embryonic development.

" Pugheadedness " (Mopsköpfe), a shortening of the snout, was noted by Letaconnoux (*op. cit.*) in several teleosts, particularly the gadoids. This condition has been reported by a number of other authors. Gudger (1930) and Raney (1952) described it in striped bass (Fig. 11), and Mann (1954) reported on the occurrence of " pugheads " among Baltic Sea pike, thought to be genetic, but possibly influenced by environmental factors such as lack of oxygen or salinity variations during embryonic life. No difference in weight was seen in such fish as compared with normal fish, but they are so often rejected by the European shopper that they are usually culled in advance. A pugheaded herring was described by Ford (1930), who also cited earlier evidence for the hereditary origin of the abnormality in fishes.

Abnormal conditions in larval fishes, some undoubtedly genetic and some due to environmental variations, are most often seen in hatcheries, but structural defects are sometimes seen in larvae and post-larvae taken in plankton collections. Experimental variation of such single factors as temperature at time of hatching can drastically modify or inhibit formation of the jaws of larvae and can cause an increase in occurrence of other gross abnormalities. Volodin (1960),

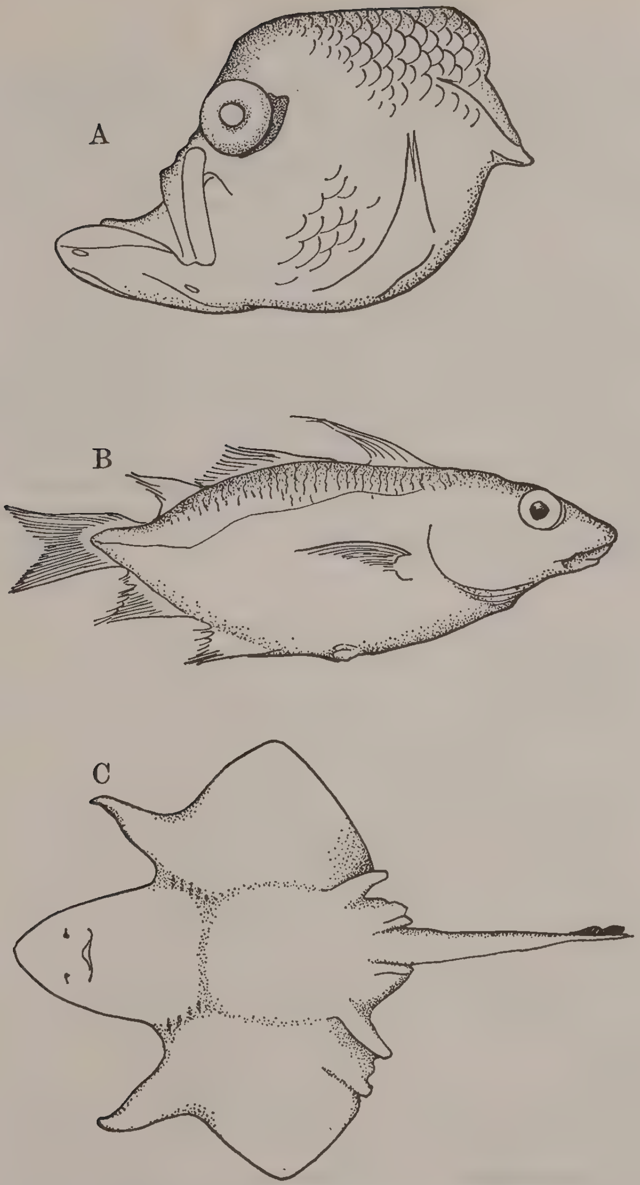

Fig. 11. Skeletal abnormalities.
(*a*) " Pugheaded " striped bass; (*b*) " Short-tailed " haddock;
(*c*) fin malformation in thorny skate.

for example, found that exposures to low temperatures (0 to 6°C) during early incubation produced malformed larvae of bream, *Abramis ballerus* L., and pike (probably *Esox lucius* L.). Sharp changes in temperature during early development could also produce malformations or death. Physiological abnormalities in larvae are less easily identified, except as they are reflected in lack of growth and death of individuals.

V. Effects of Disease

The significance of marine fish diseases may be assessed from the viewpoint of the host population or from that of the human predator. Epizootics may reduce the numbers of fish available to man, and in at least some marine species disease may be a primary mechanism for regulation of population size. Diseases that weaken or disorient fish, or make them more conspicuous, can be of great importance in determining survival of individuals. Protozoan, helminth and copepod parasites of the flesh, although not often direct causes of death, can act to weaken or slow the host and are also of great economic significance in the landed catch.

A. *Epizootics and mass mortalities*

Mass mortalities of marine, estuarine and anadromous fishes are common, even though many such events may escape scientific attention. Newspapers and interviews with fishermen would probably provide the best criteria for evaluating the extent of mortalities, except for those events that occur beyond the continental shelves. Many factors may, of course, contribute to mass deaths of marine fishes, including physical and chemical changes in the environment (Brongersma-Sanders, 1957), as well as the biological realities of starvation, predation and disease. Disease is often suspect, but has infrequently been proved without question to be a cause of mass mortalities. Too often scientific study is not made, or is made too late, or the results of the study are inconclusive. Interest in the event is usually proportional to the numbers of fish dying at the particular moment; long-term studies necessary to understand the role of suspected pathogens have rarely been carried on.

The often dramatic increase in disease prevalence that we term an epizootic is the result of interactions of such variables as susceptibility of the host population, virulence and infectivity of the pathogen, effectiveness of transmission and physical factors in the environment. Fundamentally, an epizootic of an infectious disease requires that one or more of the following conditions exist: (1) the pathogen must be newly introduced in a susceptible population; (2) infection pressure (dosage) or virulence of the pathogen must increase; or (3) resistance of the population must be lowered. The role of environmentally related influences and stresses such as nutrition, temperature and salinity on disease prevalence must also be considered. Determination of factors prevailing at the time of an outbreak requires very broadly based and continuous studies in ecology, immunology and pathology. Despite the fact that such ideal studies have not often been made in the past, an appreciable amount of documentation has been assembled for a few marine fish diseases with histories of epizootic prevalences and mortalities. Outstanding in this respect is the fungus disease of herring and other species, referred to earlier, caused by *Ichthyophonus hoferi*. Outbreaks of this pathogen in herring of the western North Atlantic have been known since 1898 (Cox, 1916; Fish, 1934; Scattergood, 1948; Sindermann, 1956, 1958). The most recent occurred in the Gulf of Saint Lawrence in 1954–55, when an estimated one-half of the herring population of that gulf was killed by the disease. The estimate was based on sampling and field observations during the outbreak, and the behavior of the fishery since then has supported the original estimate. Landings declined to about half their previous level, in the absence of other factors such as change in fishing effort or market demand. Earlier work (Cox, 1916) indicated that comparable reductions in population abundance and in the fishery followed the outbreaks of 1898 and 1914. Reports of outbreaks in the Gulf of Maine also suggested major dislocations in the fishery (Scattergood, 1948). It is interesting and perhaps pertinent that the two most recent outbreaks—the only ones for which we have adequate fishery data—occurred at times of herring abundance, as indicated by landing statistics and general observations.

One of the most remarkable aspects of the fungus disease of herring in the western North Atlantic has been its apparent periodicity—six recorded outbreaks 14 to 25 years apart (Fig. 12). The two principal areas involved, Gulf of Maine and Gulf of Saint Lawrence, each with discrete populations of herring, have been out of phase during the most recent outbreaks; an epizootic peak in one gulf coincided with very low disease prevalence in the other. The comparatively brief interval between outbreaks suggests at best only transient increase in resistance of herring populations to the disease. This hypothesis is supported: by relatively low disease prevalence (an average 27%) at the epizootic peak, which constitutes low selection pressure; by the fact that the most recent outbreak was at least as severe as the first recorded outbreak in 1898; and by determination of mortality rates in experimental epizootics of comparable intensity (Sindermann, 1958).

Another disease with an even longer history of epizootic prevalences is the "red disease" of eels caused by *Vibrio anguillarum*. Italian literature dating back to Bonaveri in 1718 (cited by Hofer, 1904) records repeated and severe outbreaks on the coast of Italy throughout the eighteenth and nineteenth centuries, and gives some estimates of numbers of eels killed. For example, Spallanzani in 1790 described an outbreak that killed almost 100 000 pounds of eels from the Comachio Lagoons on the east coast of Italy near Ravenna in one 38-day observation period. The continuing presence of the disease in Italy was reported by Ghittino (1963b). Literature from northern

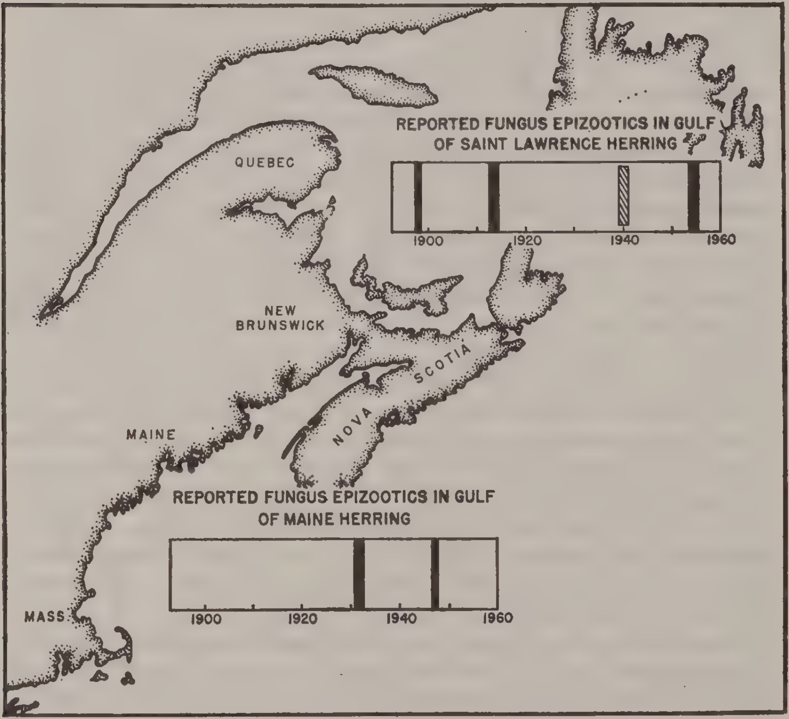
REPORTED FUNGUS EPIZOOTICS IN GULF OF SAINT LAWRENCE HERRING
1900
1920
1940
1960
QUEBEC
NEW BRUNSWICK
NOVA SCOTIA
MAINE
MASS.
REPORTED FUNGUS EPIZOOTICS IN GULF OF MAINE HERRING
1900
1920
1940
1960

FIG. 12. Reported epizootics of *Ichthyophonus* in herring of the western North Atlantic. The 1940 Gulf of Saint Lawrence outbreak is included on the basis of verbal reports from fishermen and area residents. (From Sindermann, 1963.)

Europe, particularly Scandinavia, provides other evidence of widespread epizootics in which great numbers of eels were killed (Bruun and Heiberg, 1932, 1935). An outbreak in eels of the Baltic coast of Germany in 1959, reported by Mattheis (1960), followed a period of several decades of low prevalence. Mattheis also observed that an epizootic in eels preceded by one year an outbreak in pike.

The very recent epizootic of bacterial etiology in Chesapeake Bay white perch seriously reduced the population, as indicated by field observations of shoals of dead fish, and numbers washed up on shore, as well as by a sharp decline in production. The fishery in 1964, the first post-epizootic year, was markedly reduced in comparison with previous years. Landings of white perch in 1964 were only 622 000 pounds, as compared with an average of 1 500 000 pounds for the three preceding years; no indication existed that other major variables had changed. Statements by sportsmen and local residents indicated that white perch were extraordinarily abundant in 1962, the year immediately preceding the outbreak.

Mass mortalities appear to be, and often are, catastrophic events when viewed from close proximity. Their long-term effects may be severe, even resulting in extinctions in part of the host range, or they may be slight, causing only minor depressions in population size. If reduction is severe enough and the ecological " niche " vacated long enough, the species may be replaced by another with similar ecological requirements. The original species may then persist in low abundance for a long period. This is probably the extreme consequence of disease. The more probable course of events, in view of the high reproductive potential of most teleosts, is a gradual return to former population size and only temporary disturbances of many parts of the ecosystem in which the species is enmeshed. An extensive and still emerging documentation of the degree of this dislocation can be found in studies of the fisheries in the Gulf of Saint Lawrence during and after the recent epizootic of fungus disease (Kohler, 1961; Sindermann, 1963; Tibbo and Graham, 1963). Herring were most seriously involved, and landings during the post-epizootic years were less than half their previous level (Fig. 13). Mean ages in landings decreased, growth rates increased, fewer age groups were represented in the fishery, and relative abundance of herring larvae decreased sharply. Alewives, which have been described as less susceptible to the pathogen (Sindermann and Scattergood, 1954), acquired infections and were killed in sufficient numbers to be observed. Mackerel were also heavily infected; mortalities occurred; and landings decreased during the post-epizootic years. Cod did not become infected but fed on disabled herring to such an extent that their growth rate during the epizootic period exceeded anything previously recorded. Cod landings in the southern Gulf of Saint Lawrence almost doubled during the immediate post-epizootic period, due almost entirely to increased weight of individual fish caught, rather than to increased numbers of fish taken. Lobsters, important bottom scavengers, showed a similar but less dramatic increase in growth rate. Here then were both negative and positive short-term effects of an epizootic in herring—the negative brought about by increased infection pressure and mortalities of other species, and the positive by a temporarily increased food supply for important predators and scavengers, resulting in accelerated growth of species which in this case had a higher unit value to man.

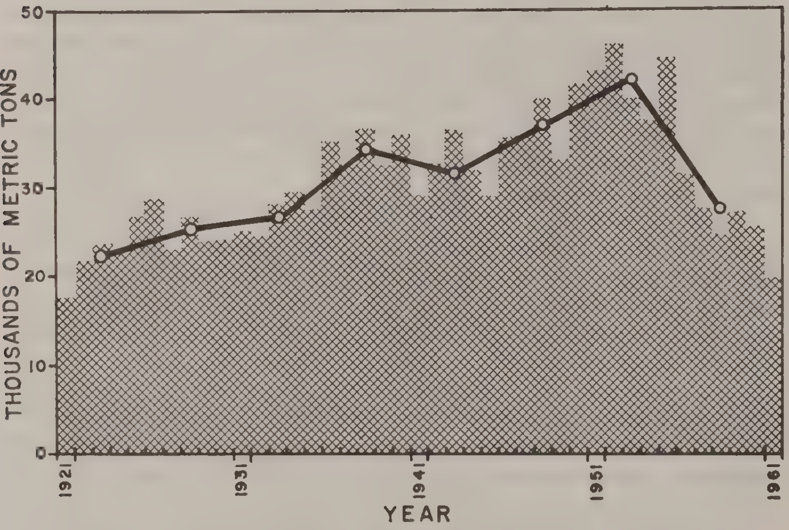

FIG. 13. Annual landings of Atlantic herring in the southern Gulf of Saint Lawrence, 1920–61. (From Sindermann, 1963.)

B. " *Background* " *effects*

Epizootics provide the dramatic and obvious examples of disease as a factor of resistance to the biotic potential of marine fishes. The more pedestrian, less conspicuous, but probably more significant effects of disease are those that have been variously described as " low level " or " background " effects. Disease may cause continuous subtraction of individuals by weakening and disorienting infected fish, reducing their ability to escape predators and to survive variations in the physical environment; by blinding fish; by making infected fish more conspicuous; or by altering behavior in ways that render fish more vulnerable to predation. A disoriented, erratic circular swimming movement at or near the surface has been observed as a generalized symptom of a number of diseases. It was first described by Plehn and Mulsow (1911) as a symptom of *Ichthyophonus* infection in European salmonids, and has since been seen during mass mortalities of Pacific and Atlantic herring. Exophthalmia, with subsequent destruction of the eye, is another generalized symptom of several diseases, including bacterial infection and larval trematode invasion. Cataracts, usually of both eyes, were noted by Raney (1952) in striped bass. Spinal curvatures, evidently of neuro-muscular origin, have also been described as generalized signs of bacterial and fungal infections. In studies of herring diseases it has been noted that individuals with bacterial infections exhibited characteristic and easily visible whitish patches near the tail. Field observations of immature herring schools disclosed that individuals so affected were easily seen even in turbid water and during twilight. Other studies brought out the fact that diseased herring aggregated differentially in deeper water, and that samples of immature members of this pelagic species taken in bottom trawls contained higher frequencies of abnormal fish than did samples taken with conventional surface gear (purse seines and gill nets) in the same areas. Bruun and Heiberg (1932) and others have noted that eels with "red disease" were lethargic and often motionless on the bottom where they could be caught easily by hand. Locomotion became disoriented and swimming became a series of stiff wriggling movements.

Examinations of fish with extensive intramuscular myxosporidean cysts and necrosis, with heavy larval nematode infestation of muscles, or with many copepods imbedded in their flesh, lead inevitably to the conclusion that such a parasite burden, although it may not be the primary cause of death, must seriously reduce statistical chances for survival in an environment in which early and sudden death is the rule. Disease may also reduce the reproductive capacity of marine fish populations. Castration has been reported (Pinto, 1956) in European sardines as a result of invasion of the testes by *Eimeria sardinae*. Later studies disclosed that over 50% of the individuals sampled were parasitized. Mechanical interference with the discharge of sex products can result from massive visceral infections of smelt by *Glugea hertwigi*. Cysts of the parasite occupy much of the body cavity, occlude the vent and prevent normal spawning.

C. *Economic effects*

Economic effects of disease in marine fishes may be categorized as follows: reduction in numbers of food fish available to the fishery; weight loss of individuals; rejection by consumers and subsequent loss of interest in fishery products as food; and indirect effects, either favorable or unfavorable, on survival of other species in a food chain. Examples of economic effects in each of the categories have been mentioned throughout this paper.

Second only to mortality induced directly or indirectly by disease is the often significant weight loss of diseased fish. Williams (1963) has drawn attention to possible losses of thousands of pounds of fishery products annually because of nutrient requirements of fish parasites or disruption of the host's metabolism by disease organisms. *Lernaeocera branchialis*, for example, usually causes significant weight loss, so that parasitized fish are 20 to 30% below average weight. This loss can be an important economic factor if 50 to 80% of fish landed are parasitized, as is often true.

Rejection of diseased fish by dealers or consumers can also be economically important. Mann (1954) has summarized some of the economic effects of parasites and diseased conditions of fish from the eastern North Atlantic; he dealt particularly with fish as they appear on the market. He indicated that protozoans, larval nematodes and tissue-invading copepods created the most serious problems. Cited as an example was microsporidean (*Glugea stephani*) infection of the intestine, gall bladder, liver and mesenteries of plaice. The parasitized fish gradually became thinner, probably due to destruction of digestive epithelium. Also considered was another microsporidean, *Plistophora ehrenbaumi* Reichenow, which caused destruction of somatic muscles of catfish, *Anarrhichas lupus*, and produced large unsightly tumors. Mann mentioned a large catch of catfish landed at Hamburg in 1952, from West Iceland waters, of which 10% had to be discarded as unsuitable for human consumption. Ulcers and cysts caused by *Sphyrion* invasion of redfish and other species make it necessary to remove the diseased areas during processing. Since up to 25% of the catch may be parasitized, the filleting operation is slowed and many pounds of fillets must be discarded. Because of high frequency and intensity of parasitization of redfish in the Gulf of Maine, the resulting increase in processing costs, and the decrease in processed yield, it may soon be necessary to downgrade the species in that area from a food fish to an industrial fish, utilized only as a source of fish meal and oil.

Hargis (1958) has cited very interesting data from fish processors, indicating that candling and trimming to detect and remove flesh parasites can increase costs of packaging up to 80%. Of particular significance were *Sphyrion* " buttons " in redfish, *Porrocaecum* larvae in cod, and *Stephanostomum* metacercariae in flounders.

Larval nematodes are most likely to produce consumer complaints if found in marketed fish. *Eustoma* (*Anacanthocheilus*) larvae occur in mesenteries and gonads of European herring. Mann (1954) reported them as infrequent in small herring but common in adult herring of the Norwegian coast. Larval Anisakinae are also common in herring of the North American east and west coasts. Larval nematodes invade the liver of gadoids, disrupt normal function and often cause extensive atrophy. This condition is prevalent in haddock, where larval worms may occur in the flesh as well. Presence of conspicuous larval cod worms (*Porrocaecum*) in the flesh can lead to rejection of infested fish. Certain inshore grounds off Canada have not been fished for cod because of a history of consistently high nematode parasitization.

VI. Variations in Disease Prevalence

Description of the role of disease in marine fish populations must include consideration of the dynamic relationships of host, parasite and environment. Some of the consequences of these interactions are reflected in variations in the occurrence or prevalence of particular diseases with age of the host, with geographic location within the host's range, and with time. Thus, a disease may be characteristic only of juveniles or only of adults; it may occur in one gulf and be absent in another; or it may be abundant today and very rare ten years from now. Examples of such variability are available, although the underlying causes are sometimes obscure.

A. *Geographic variations*

Evidence has accumulated to provide a reasonable picture of geographic variations in the occurrence and abundance of the parasitic copepod *Sphyrion* in redfish of the western North Atlantic. Major centers of abundance exist in the Gulf of Maine and off the coast of Labrador; minor centers occur on the south-east slope of the Grand Bank and in the south-eastern Gulf of Saint Lawrence. The parasite is absent from other major fishing banks of the western North Atlantic. Templeman and Squires (1960) have reviewed possible reasons for such marked variations, which apparently persist from year to year. Redfish do not undertake extensive migrations and are closely associated with the bottom; both factors may be important in maintaining enzootic centers of infestation.

Studies have been made during the past decade of parasitic diseases of sockeye salmon primarily as an aid in identifying the continental origin of high seas stocks. Margolis (1963), who summarized these studies, reported that certain parasites were peculiar to Asian stocks and others to North American. Over 50 species of parasites were encountered in the survey, many of which varied locally or seasonally, and some of which occurred throughout the range of the host species, although in different frequencies. A larval cestode, *Triaenophorus crassus* Forel, was found in the flesh of salmon from Bristol Bay, but was absent from Kamchatkan samples. Conversely, an adult nematode, *Cucullanus truttae* (Fabr.), was found in Kamchatka and Okhotsk Sea samples, but was absent from North American samples.

Highly localized variations in abundance of disease were seen in myxosporidean (*Kudoa clupeidae*) infection of Atlantic herring in the Gulf of Maine. A sharp discontinuity existed on the Maine coast, documented for ten years (Sindermann, 1965), in which 1-year-old fish were commonly found to be infected on the western coast and were never found to be infected on the eastern coast. This difference has been attributed largely to summer sea water temperatures, although other factors may be involved. The discontinuity was so distinct that cysts of the parasite have been used as natural tags to trace subsequent movements of immature fish. The gall-bladder-inhabiting Myxosporidea of whiting have been found to vary in abundance geographically in the North Sea (Kabata, 1963b). *Ceratomyxa arcuata* Thélohan occurred in 46% of whiting sampled in the northern North Sea, while *Myxidium sphaericum* Thélohan infection was only 1·3%. The reverse was found in the southern North Sea, with *Myxidium* reaching an average of 40% while *Ceratomyxa* averaged only 9%. This suggested the existence of two North Sea whiting stocks—a conclusion supported by meristic data.

Broader geographic variations in parasite frequencies were disclosed in a study of the distribution of larval cestodes (Trypanorhyncha) in adult herring from the north-west Atlantic. The parasites were absent in four years' sampling from the Gulf of Saint Lawrence, but increased in frequency with decreasing latitude (Fig. 14). A strikingly similar situation prevails in the Pacific. Dogiel (1955) observed that mintai or Alaska pollock, *Theragra chalcogramma*, which are heavily parasitized by larval cestodes from sharks, harbored far fewer worms in Kamchatkan waters than in Japanese waters. Variations such as these are undoubtedly related to distribution and abundance of the elasmobranch definitive hosts.

Differences of a comparable geographic scale were reported for two coccidians, *Eimeria sardinae* and *E. clupearum*, in herring. Polyanski

(1955) reported *E. sardinae* but not *E. clupearum* in Barents Sea herring. Kabata (1963a) found both species in North Sea herring, while Shulman (1959) found *E. sardinae* in the Gulf of Riga but not in the Gulf of Finland. Changes associated with salinity have been observed in the occurrence of other parasites of White and Baltic Sea herring (Shulman and Shulman-Albova, 1953; Dogiel *et al.*, 1958). Several stages in the transition from strictly marine to fresh-water parasites were noted in the surveys involved.

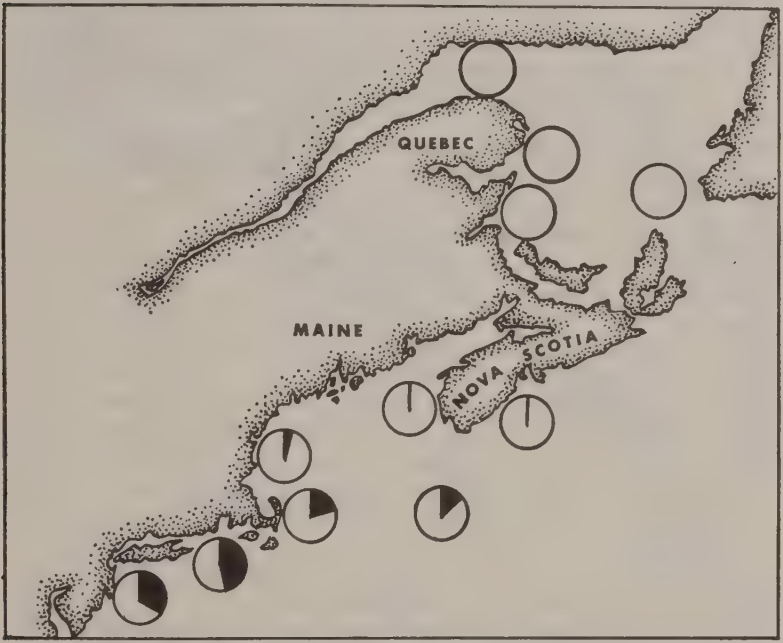

Fig. 14. Prevalence of larval cestodes (Trypanorhyncha) in Atlantic herring (percentage infestation in black).

Other herring parasites have been examined from widely separated locations in the North Atlantic and adjacent waters (Shulman and Shulman-Albova, *op. cit.*; Dollfus, 1956; Sindermann, 1961a). Specific locations within the hosts on either side of the Atlantic are sometimes occupied by a nucleus of similar but not always identical parasites, whereas each geographic area also superimposes its own variety of parasites because of salinity differences, presence of intermediate or definitive hosts, temperature differences, diet, depth and other factors.

As examples, the myxosporidean *Kudoa clupeidae* has been reported from herring of the western Atlantic but not the eastern, the larval nematode *Eustoma rotundatum* from the eastern but not the western Atlantic, while parasites such as the coccidia mentioned above and the trematode *Brachyphallus crenatus* (Rud.) occur in varying frequencies on both sides of the Atlantic.

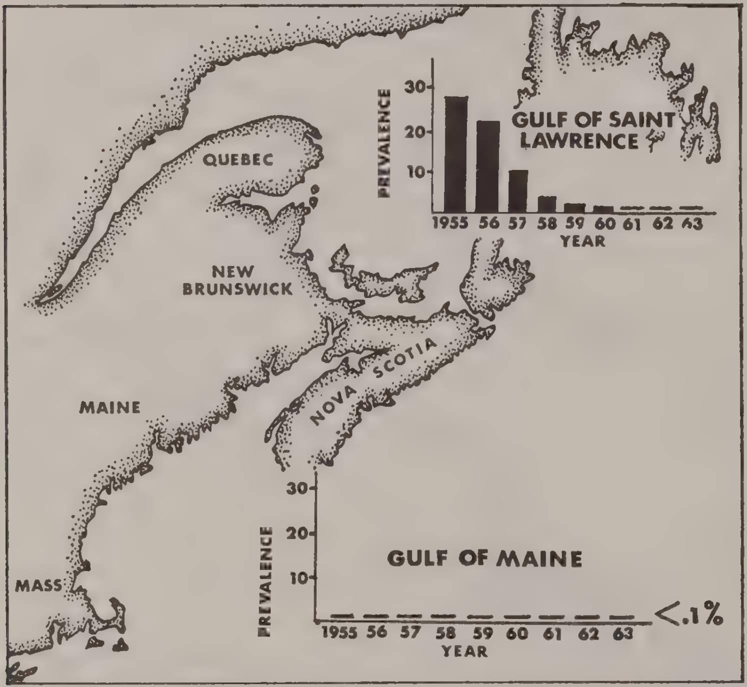
PREVALENCE
30
20
10
1955 56 57 58 59 60 61 62 63
YEAR
GULF OF SAINT LAWRENCE
QUEBEC
NEW BRUNSWICK
NOVA SCOTIA
MAINE
MASS
PREVALENCE
30
20
10
GULF OF MAINE
<.1%
1955 56 57 58 59 60 61 62 63
YEAR

FIG. 15. Prevalence of *Ichthyophonus* in Atlantic herring of the Gulf of Saint Lawrence and the Gulf of Maine, 1955–63.

B. *Temporal variations*

Temporal variations in prevalence of disease are most apparent in studies of epizootics. Unfortunately, long-term studies of prevalences have rarely been carried out, so that the annual increases in incidence building to epizootic levels, or the subsequent annual declines in disease abundance following epizootics, have rarely been documented for marine fish populations. Referring again to *Ichthyophonus* disease of western North Atlantic herring, the general sequence of events that has emerged from studies of several outbreaks includes a long enzootic phase of very low prevalence ($< 0{\cdot}1\%$), several years of rapidly increasing incidences reaching an epizootic peak when about 25% of individuals are infected and acute infections are common, then several years of rapidly declining incidences and return to the enzootic phase. Annual sampling since the most recent outbreak in Gulf of Saint Lawrence herring has provided some data to support these general observations (Fig. 15). The consistency in this sequence of events, as deduced from fragmentary observations during the years immediately preceding and following the epizootics of 1931, 1947 and 1954 suggests that future outbreaks of *Ichthyophonus* disease may be predicted several years in advance, if sampling of herring populations is continuous.

Other diseases of herring have not exhibited the periodicity characteristic of the fungus disease. Continuous sampling for myxosporidean (*Kudoa*) infections has disclosed only minor variations in prevalence in those areas where the parasite occurs. It is of course possible, and even likely, that longer-term variations in abundance might be expected for this and other parasites. Similar stability in parasite abundance has been found in a 5-year study of larval nematodes (Anisakinae) and larval cestodes (Trypanorhyncha) in herring from the North American east coast.

Other examples of dramatic increases in abundance of pathogens and parasites can be found in the literature. Dogiel and Lutta (1937) studied such an outbreak in sturgeon caused by monogenetic trematodes introduced into the Aral Sea with their normal hosts. Increases of this kind are often seen in marine aquaria, and are considered in a later section.

C. *Age effects*

The effect of host age on the parasite fauna has been examined repeatedly. Recent summarizations of Russian work (Liaiman, 1955; Polyanski and Shulman, 1956; Polyanski, 1958) indicate that significant variations with age can result from segregation into schools of similar age that often occupy different habitats at different ages, and from changes in diet of fish with increasing age. Increase in occurrence and intensity with age is often characteristic of worm infestations, but is not necessarily true with microbial agents, many of which may be more common in young fish than in old. Polyanski and Shulman (*op. cit.*) have described the changes with age in the parasite fauna of cod and Reshetnikova (1955) of mullet in the Black Sea. The authors made the point that "juvenile" parasites, characteristic of very young individuals, are replaced by parasites typical of adult hosts, due to lack of association of juveniles and adults, change in habitat from inshore to offshore, and change in feeding habits and diet.

Studies of Atlantic herring (Sindermann, 1963) have further demonstrated age-associated changes in parasite fauna. The body wall overlying the visceral cavity of post-larvae is sometimes infected with a species of *Plistophora* which has not been found in juveniles over 6 months old. Juvenile herring between 6 months and 1 year old harbor an adult cestode not seen in older fish. Juveniles between 9 months and 3 years are infected with the myxosporidean *Kudoa clupeidae*, which is absent in adults. Larval trematodes, *Cryptocotyle lingua*, are characteristic of juvenile herring because the young fish live during the warmer months in close proximity to intertidal snail populations (Sindermann and Farrin, 1962). Adult herring, which are only lightly infested, remain farther offshore except during spawning. Other parasites—larval cestodes (Trypanorhyncha) and larval nematodes (Anisakinae)—make their first appearance in juveniles about 1 year old and, depending on geographic area, gradually increase in abundance with increasing age.

Disease may begin to exert effects very early in the life history of the fish. Eggs of marine fishes are often coated with microorganisms; Oppenheimer (1955) found that hatching percentages of cod, turbot and sardine eggs were increased in bacteria-free media. Ahlstrom (1948) found abnormalities, some of which may have been disease-induced, in as many as 45% of developing Pacific sardine eggs.

VII. Immunity

Resistance to fish diseases involves a complex of interacting factors, including individual variability, species characteristics, seasonal influences and nutritional effects. Immunity has both cellular and humoral aspects and extends from obvious phagocytic, lytic and agglutinating activity to include such factors as the role of skin and mucus barriers and the role of gastric secretions. Some of the mechanisms of natural and acquired resistance to disease in fish have been summarized by Bissett (1947a, 1947b), Dreyer and King (1948) and Snieszko (1958); McDermott (1956) and Hirsch (1959) have reviewed the cellular and humoral mechanisms of immunity.

A number of papers have appeared recently which clearly substantiate earlier findings (Blake and Anderson, 1930; Toth, 1932; Nybelin, 1935a; Schäperclaus, 1938; Snieszko *et al.*, 1938; Smith, 1940) of specific immunological competence in fish. Clem and Sigel (1963), Sigel *et al.* (1963), and Sigel and Clem (1965) studied immune responses in marine teleosts and elasmobranchs to injected viral and bacterial antigens. Lemon shark, *Negaprion brevirostris* (Poey), produced significant titers of hemagglutination-inhibition antibodies with a high degree of specificity in response to injected influenza virus. Lower titers and less specificity were found in similar studies of the margate, *Haemulon album* Cuvier. A very low degree of immunologic reactivity was evident in the sea lamprey, *Petromyzon marinus* L. Goncharov (1962) hyperimmunized several cyprinid species at 15 to 25°C with killed *Pseudomonas fluorescens* and other bacteria, and produced agglutinin titers as high as 10 240. The agglutinins were specific, and the reaction was temperature-dependent, since antibodies were not formed at 6 to 7°C. Krantz *et al.* (1963, 1964), in research oriented toward control of hatchery diseases through immunization, reported significant antibody response in trout to killed bacteria injected with adjuvant. Maximum agglutinin titers were reached 3 to 4 months after injection. Fish immunized with a vaccine of formalin-killed *Aeromonas salmonicida*, the etiological agent of furunculosis, were protected during challenge with viable pathogens, but untreated controls were not. The authors pointed out, however, that augmented natural defense mechanisms often cannot prevent infection when the fish is confronted by severe physiological or environmental stresses. Post (1963) had used a similar immunization method to achieve moderate protection of rainbow trout, *Salmo gairdneri*, against *Aeromonas hydrophila*.

Spence *et al.* (1965) were able to produce appreciable antibody titers in rainbow trout immunized against *Aeromonas salmonicida*; the antiserum so produced provided passive protection of juvenile salmon when injected intraperitoneally. Several authors, including Post (1962) have suggested oral immunization as a practical mass prophylactic method, but evidence is conflicting. Duff (1942) reported resistance of trout to furunculosis after feeding an oral vaccine of killed *Aeromonas salmonicida*, and Ross and Klontz (1965) found increased survival of rainbow trout after oral immunization against " redmouth disease." Snieszko and Friddle (1949), however, were unable to demonstrate protection of young brook trout against furunculosis by oral immunization and Spence *et al.* (1965) found that oral vaccine did not protect salmon exposed to *Aeromonas salmonicida*.

Poikilothermic vertebrates such as fish are excellent subjects for basic studies of immune responses. Allen and McDaniel (1937), Pliszka (1939), Cushing (1942) and Bisset (1946, 1948a, 1948b) have summarized effects of temperature on antibody production, and have demonstrated that production was minimal below 10°C. Sindermann and Honey (1964) found that certain natural heteroagglutinins of winter skates, *Raja ocellata* Mitchill, varied seasonally, with minimum titers at times of minimum environmental temperatures. Hildemann (1957) noted acceleration of rates of homograft rejection in fish coincident with increasing environmental temperature. The immune response was measured by survival time and inflammatory reactions. Duration and intensity of inflammation were closely associated with rapidity of donor-tissue destruction. Fine and Drilhon (1961) demonstrated the formation of precipitins in eels in response to injections of human serum. Wolf (1941, 1954), Snieszko (1957b) and Ehlinger (1964) found differences among strains of brook trout, *Salvelinus fontinalis*, in resistance to ulcer disease and furunculosis. Papermaster *et al.* (1964), in studies of the evolution of immune responses, found a rising level of reactivity and complexity as the phylogenetic scale from hagfish to teleost was ascended.

Goncharov (1959a) reported high antibody titers in fish immunized against *Achromobacter punctatum* (*Pseudomonas punctata*), and also pointed out the prevalence of cross agglutinations in work with such immune sera. Earlier, Mann (1939) had shown that carp affected by ascites (Bauchwassersucht) developed high agglutination titers against *Pseudomonas punctata*, but Roegner-Aust *et al.* (1950) and Goncharov (1959b) presented arguments that a virus was the primary etiological agent. Sorvachev *et al.* (1962) described prophylactic immunization of carp with an attenuated virus vaccine. According to their report, the 1- and 2-year-old progeny of hyperimmunized carp suffered little mortality during a severe outbreak of ascites, whereas young of unvaccinated fish died in great numbers. Such findings are unique, and are more suggestive of maintenance of immunity by natural infections. Despite some continuing disagreement about the causative organism, summarized by Schäperclaus (1965) and others in a recent symposium (Snieszko *et al.*, 1965), a body of literature on the epizootiology of this very important disease of carp has accumulated. Included are indications of acquired immunity after infection, a possible role of bacteriophage, changes in virulence and adaptation to new hosts—all problems that may be pertinent to certain marine fish diseases.

Fungus or myxosporidean invasion of fish often produces only tissue destruction with little indication of host inflammatory response. Intramuscular parasites may cause hyalinization and lysis of muscle tissue until only granular debris and spores remain. In some individuals, however, fungus invasion elicits extensive formation of fibrous connective tissue by the host (Fig. 16).

Evidence of local immunity to monogenetic trematode infestation

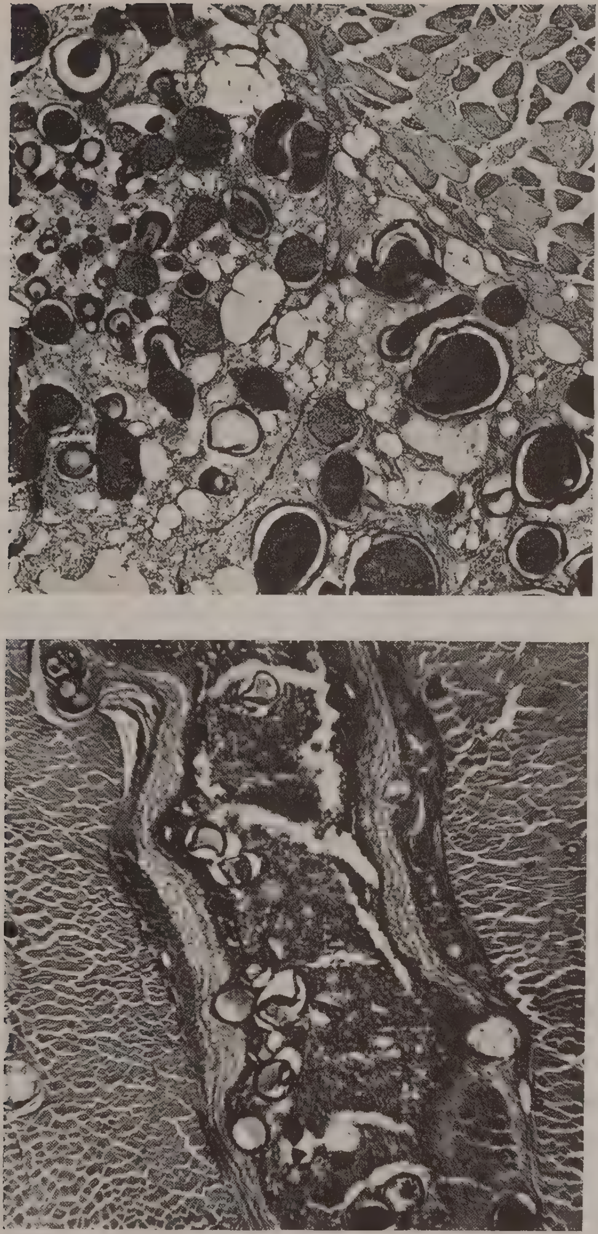

Fig. 16. Host response in acute (above) and chronic (below) *Ichthyophonus* infection of the body muscles of Atlantic herring.

has been described by several authors. Jahn and Kuhn (1932) reported heavy infestation of eyes of Serranidae and Lutianidae by the monogenetic trematode *Benedenia melleni* (MacCallum). Aquarium fish carried up to 2 000 worms, attached to eyes, gills and nasal cavities, and were frequently killed. Survivors usually harbored progressively fewer parasites; this decrease was attributed to development of local immunity and to immune mechanisms of the host mucus (Nigrelli and Breder, 1934; Nigrelli, 1935a, 1935b, 1935c, 1937, 1947). Immunity to other helminth parasites of fishes has not been demonstrated.

VIII. Diseases in Marine Aquaria

Disease control has become of increasing significance with the establishment of many new marine aquaria, oceanaria and hatcheries, where marine fishes are caught, often at great expense, and held in captivity or actually reared under hatchery conditions. Whatever their original purpose, such artificial conditions should prove to be fruitful sources of information about diseases and epizootics in marine fishes and should also provide the needed stimulus to develop understanding of the pathogens concerned. A new technology of treatment of marine fish diseases, including many modifications of techniques used in fresh-water hatcheries and aquaria, is slowly developing (Nigrelli, 1943; Laird, 1956; Chlupaty, 1962; DeGraff, 1962; Højgaard, 1962; Oppenheimer, 1962; Paccaud, 1962) and should expand greatly in the next decade.

As has been true in fresh water, many of the real advances in understanding the role of fish diseases in the sea can be expected from studies of individuals in captivity. This has been and will be true especially of the infectious diseases, which may in epizootic form sweep through aquarium populations, or in enzootic form result in continued attrition of valuable specimens. Several references to diseases in aquarium environments have already been made in this paper.

Infectious diseases are easily imported with fish from natural habitats, and flourish in an artificial environment because of increased effectiveness of transmission from fish to fish in a restricted body of water, because of somewhat higher environmental temperatures, or because of inadequate diet and consequent reduction in resistance. Fish in captivity are subject to much closer scrutiny than is ever possible in the sea, so abnormalities are more likely to be observed. Also, the absence of predators in most aquarium situations permits abnormal individuals (for example fish with advanced tumors) to live far beyond what would be their survival time in nature. As pointed out by Oppenheimer and Kesteven (1953), external symptoms of bacterial infections are often visible only when the fish is under water. These infections can best be seen in captive fish—in fact most of the bacterial diseases of marine fishes, such as dermatitis and tuberculosis, have been observed in captive populations (Aronson, 1926; ZoBell, 1946; Nigrelli and Vogel, 1963). Bacterial pathogens, because of high infectivity and short generation time, are observed most commonly and produce severe effects in marine aquaria. Oppenheimer and Kesteven (1953) reported that of all external lesions in salt water aquaria, bacterial tail rot or fin rot was most common. This has been the author's conclusion also, based on ten years' observations of herring held in captivity for varying periods up to two years. The disease syndrome included progressive erosion of fins and tail, minute hemorrhages beneath scales, disorientation and roughening and raising of the integument. *Pseudomonas ichthyodermis*, the pathogen involved in Oppenheimer and Kesteven's study, reached epizootic proportions during summer, and many species of fishes were infected.

Other examples of skin ulcerations and fin rot of bacterial origin in captive fishes were reported by Anderson (1911), Riddell and Alexander (1911), Wells and ZoBell (1934), Sindermann and Rosenfield (1954a) and Conroy (1963). Oppenheimer (1958) described a progressive tail rot disease of cod, *Gadus morhua* L., held in live boxes, accompanied by bacteremia and death usually within 48 hours from onset of symptoms. Reinfections were obtained from cultured bacterial isolates, and the causative organism was characterized as a species of *Pseudomonas*. The disease developed in water temperature of 5 to 9°C, and Oppenheimer's description of symptoms is remarkably similar to that for herring. An interesting paper by Ford (1928) discusses tail abnormalities in young herring that are highly reminiscent of the effects of bacterial disease, but which are attributed by the author to " nibbling " by other members of the school.

Lymphocystis disease is not uncommon in marine aquaria. Nigrelli and Smith (1939) noted that the disease was most abundant in summer and disappeared in winter. Successive individuals exhibited symptoms but most infected fish recovered.

" Velvet disease " of marine fishes caused by the dinoflagellate *Amyloodinium ocellatum* (Brown) has assumed epizootic proportions in aquaria (Brown, 1934; Brown and Hovasse, 1946). Heavy mortality occurred for three years in the aquarium of the Zoological Society of London. Both cold-water and subtropical fishes were affected and mortalities began soon after arrival of specimens from Bermuda. Primary cause of deaths was the parasitic dinoflagellate *Amyloodinium* *ocellatum* on the gills and occasionally the external surfaces of 28 species. The parasite appears to be nonspecific in host selection. Laird (1956) reported it as a cause of major mortalities in a Singapore aquarium. Primarily a gill parasite, it caused hemorrhages and adhesions of gill filaments and interfered with host respiration. In heavy infections it spread over skin and fins, giving the appearance of powdery or velvety patches. Nigrelli (1936) also reported this parasitic dinoflagellate as common on skin and gills of many species in marine aquaria.

A ciliate parasite, *Cryptocaryon irritans* Brown, is the marine counterpart of the ubiquitous fresh-water *Ichthyophthirius multifiliis* Fouquet. The parasite, only briefly described by Brown (1951), causes " white spot disease " because of whitish pustules formed on gills and epidermis (Fig. 17). Epizootics caused by *Cryptocaryon* have been described in marine aquarium fishes in Japan, London and Singapore (Brown, 1951; Laird, 1956). Heavy infections were rarely seen in natural populations. In Fiji, only one species, the rock cod, *Epinephelus merra* Bloch, was infected of 36 species examined from the same coral reef, and all infections were very light (Laird, *op. cit.*), but in aquarium epizootics few species were immune to infection. In Japan 44 of 53 aquarium species were attacked (Sikama, 1938). Parasite numbers increase rapidly when the mature trophozoite drops off the host and encysts on the aquarium bottom. Multiple divisions that follow produce large numbers of motile infective stages.

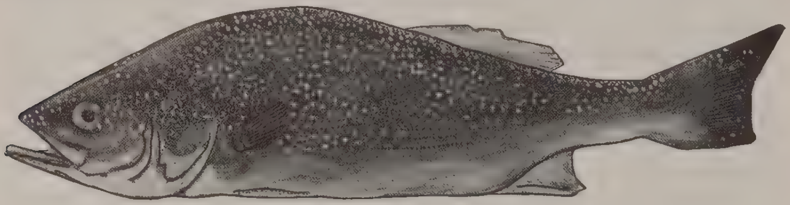

FIG. 17. " White spot " disease of seatrout. (After Sikama, 1938.)

The emergence, in the aquarium environment, of other pathogens virtually unknown in fish from natural habitats is well illustrated in a series of studies carried out in the aquarium of the Oceanographic Institute of Monaco. Two algae, *Leucosphaera Oxneri* and *Thallamoebella parasitica*, were described by Raabe (1937, 1940a, 1940b) as responsible for epizootics and mortalities in a number of marine fish species. Other parasites, including Microsporidea and larval nematodes, were also indicted in aquarium mortalities (Raabe, 1936; Guiart, 1938). Earlier, Russell (1923) reported lesions and emaciation due to heavy infestations of the copepod *Caligus pageti* on grey mullet, *Mugil capito*, kept in experimental ponds in Egypt. The parasite had not been seen previously in wild populations.

IX. Relationship of Fish Diseases to Human Diseases

An inescapable aspect of any discussion of fish diseases is their possible relationship to human disease. Examples from the freshwater environment, such as the tapeworm *Diphyllobothrium latum* (L.), the nematode *Gnathostoma spinigerum* Owen, and the trematode *Clonorchis sinensis* (Cobbold), clearly demonstrate the role of fish in transmitting human parasites (Cameron, 1945). Fortunately, few examples can be found for a similar role for marine fishes. Recent reports from The Netherlands (van Thiel *et al.*, 1960; Kuipers, 1964) describe severe reactions to invasion of the wall of the human digestive tract by larval nematodes of the family Heterocheilidae, ingested alive with lightly salted herring. The disease, described as eosinophilic phlegmonous enteritis, is relatively rare, even in a population that consumes countless numbers of herring. Williams (1965) has recently summarized the available information on " herring worm disease ". His opinion is that larval nematodes other than *Eustoma rotundatum* may be agents of the disease, and that care must be taken in attempts to identify larval nematodes from the human intestine.

Eosinophilia has long been associated with many helminth infestations, and ingestion of raw fish has recently become a suspected route of transmission in outbreaks of human eosinophilic meningitis in the Pacific area (Rosen *et al.*, 1961, 1962). A possible etiologic agent is the larva of the nematode *Angiostrongylus cantonensis* (Chen), which matures in the lungs of the rat after first invading the brain (Alicata, 1965). Infestation of the mammalian definitive host—normal or abnormal—can result from ingestion of a molluscan intermediate host or a paratenic host harboring third-stage larvae. Cheng and Burton (1965) have demonstrated that oysters and clams can serve as experimental intermediate hosts and that first-stage larvae concentrated from the feces of infected rats could survive for 27 hours in salinities of 20‰. Although some epidemiological association of consumption of raw fish with meningitis outbreaks in areas of the South Pacific has been made, the role of *Angiostrongylus* is less clear, as has been pointed out by Jacobs (1963).

Larval trematodes, *Heterophyes heterophyes* (Siebold), infective to man, occur on the integument or in the flesh of mullets, *Mugil cephalus* and *Mugil japonicus*, found in brackish water (Belding, 1942). It is likely that other heterophyid metacercariae from estuarine and inshore fish may occasionally infest man. Larval tapeworms, *Diplogonoporus grandis* (Blanchard), infective to man, occur in marine fishes of Japan. Larval *Diphyllobothrium latum* infest pike and turbot in brackish waters of the Baltic Sea (Engelbrecht, 1958), and are dangerous parasites of man.

Among the human illnesses associated with infectious agents of marine fish origin are severe inflammations of superficial wounds among fish handlers due to the bacterium *Erysipelothrix insidiosa* (Trevisan) as described by Sheard and Dicks (1949), Wellman (1950, 1957) and Langford and Hansen (1954). Processing plant employees may be temporarily incapacitated by these infections, which are particularly common after injury by spines of such fish as sea robins or redfish. The causative organism has been isolated repeatedly from fish slime (Sneath *et al.*, 1951; Price and Bennett, 1951). Oppenheimer and Kesteven (1953) and Wellmann (1957) found that known strains of the bacterium grew well in sea water medium.

Recent studies in Japan (Aiso and Matsuno, 1961; Sakazaki *et al.*, 1963) have implicated the ingestion of raw marine fishes from inshore waters in summer outbreaks of human digestive disturbances. The causative agent has been identified as *Vibrio parahemolyticus* (Fujino). Although not recognized as pathogenic to fish, the organism has been isolated from the body surfaces and digestive tracts of live fish immediately after capture. It does not seem unlikely that increasing conditions of estuarine and inshore pollution could lead to an increasing role of inshore fishes in transfer of human pathogens. As long as raw marine products from inshore waters are eaten by humans, the possibility of disease transmission, either mechanically or as a result of multiplication of a pathogen within the marine host, must be recognized. Glantz and Krantz (1965) have used serotyping of *Escherichia coli* to show a relationship between bacterial isolates from fish and pollution of water. Bacteria of human origin were retained in the digestive tract of fish for short periods, but experimental studies disclosed no illness in fish fed on *E. coli* serotypes pathogenic to man.

X. Future Studies of Marine Fish Diseases

Because of the complexity and enormity of the marine ecosystem, disease problems in fish are difficult to approach. As with other marine problems, it is likely that greatest advances will be made when descriptive studies can be combined with experimentation in circumscribed bodies of water such as aquaria, salt ponds, and artificially restricted estuaries and other arms of the sea. The recent demonstration of specific immunological competence in fish further indicates that controlling factors in epizootics are not fundamentally different from those for other vertebrate groups. Individual variability in susceptibility to pathogens has been demonstrated, and the course of certain fish diseases shown to be alterable by environmental factors such as temperature and diet.

Little basis exists for pessimism as to the possibility of disease control in the sea, despite the seeming immensity of the problem. True, we now stand in marine disease studies almost where our ancestors of the Middle Ages did when confronted with the great pestilences of those days. Yet the advances made since then in understanding and control of human diseases suggest that technology and techniques impossible to foresee now can lead to manipulation of the marine environment and the factors that influence population size of marine fish. Some approaches have already been suggested. Certain diseases of inshore species (such as *Ichthyophonus* disease of herring) might be artificially supported at a level just high enough to maintain population resistance at a point where epizootics would not occur. It might be possible to overfish a population deliberately as soon as evidence of an incipient epizootic is discovered. These methods are, of course, based on present knowledge and do not constitute a legitimate portrayal of future control based on the acquisition of new information.

The severe effects of epizootics on marine fish populations have been partially documented for *Ichthyophonus* disease of herring, red disease of eels and *Pasteurella* disease of white perch. Significant reduction in population size was indicated in each outbreak by reduced catches during the post-epizootic periods. It is tempting to speculate on the basis of these observations that certain of the unexplained major past fluctuations in abundance of commercial marine species may have been caused by disease. As an example, drastic decline in mackerel abundance on the Atlantic coast of North America in the late nineteenth century may have been related to disease. During the 1954–55 fungus-disease epizootic in herring of the Gulf of Saint Lawrence, mackerel were found to be susceptible and heavily infected. Mackerel landings in the southern Gulf declined at that time to half their previous total, and have remained low to the present time. Available catch records for mackerel of the western North Atlantic, beginning in 1804, show periodic fluctuations which have been correlated with deviations in air temperatures by Taylor, Bigelow and Graham (1957), but which may well have had more immediate causes, such as periodic epizootics. It seems logical that wherever unexplained catastrophic declines in a fishery have occurred, disease must be strongly suspected. It is easy, however, to over-extend any point of view, so there is no implication here that every decrease in abundance can be blamed on disease.

Although supporting data are sometimes inadequate and fragmentary, the author believes that the following hypotheses about the role of disease in marine fish populations can be stated:

(1) Disease may exert profound effects on population size, and may at times be one of the most important factors of environmental limitation to the biotic potential of certain marine fish species.

(2) Epizootic disease in one species may have pronounced negative or positive effects on other species—predators, scavengers or competitors.

(3) Disease levels may be influenced by a number of factors, including change in susceptibility of the host population, or increase in infection pressure on the host population.

(4) Certain diseases and parasites common in one geographic area may be rare or absent in other areas. Microhabitats within hosts with cosmopolitan distribution may be occupied by different representatives of a genus or family of parasites in different parts of the world.

(5) Some of the great past fluctuations in sea fisheries may have been caused by disease.

(6) Epizootics in marine fishes may occur at times of high population density.

(7) Disease may affect fish of any age. There are some indications that earliest life history stages—eggs, larvae and juveniles—may at times be seriously affected.

(8) Close scrutiny of a marine fish species usually discloses one or more diseases which might be considered "characteristic" of that species in a given geographic area, although other diseases may occur.

(9) At least some disease problems in marine fish populations seem amenable to solution.

Although it is difficult to predict the future course of research and the development of knowledge about marine fish diseases, it is comparatively easy to itemize areas that require exploration. One of the greatest needs is for continuity of observations, so that changes in prevalence of recognized diseases, particularly those known to occur in epizootic proportions, can be documented over extended periods. These observations should be accompanied by detailed studies of such factors as food and temperature in the environment of host populations and of mechanisms of resistance to known pathogens. Acquisition of continuous information about the size of the host populations would also be an important facet of the studies.

Another critical question concerns the effects of disease on the very early life history stages of fishes. It is generally accepted that much of the mortality of a given year class occurs in the embryonic and larval stages. Variables such as oxygen, temperature, salinity and food supply are undoubtedly important, as is the very obvious and extensive predation on eggs and larvae. Effects of disease, which may also be significant, are less clearly understood, but are amenable to descriptive and experimental studies.

Another research area deserving greater attention concerns the role of viruses and bacteria in marine fish populations. Enough evidence is already available to prove that bacteria can be significant primary or secondary invaders, and causes of mortality in natural as well as captive populations. Identification of bacterial pathogens is not simple; the classification is at present confused; reinfection from cultured organisms is often unsuccessful; and disease-free experimental fish that have not been exposed in the past to the same or related organisms may be very difficult to obtain. Other basic and related problems immediately present themselves—such as the role of marine bacteriophages in populations of bacteria potentially pathogenic to fish (Spencer, 1963), and the role of antibiotics elaborated by many marine organisms in suppressing bacterial populations (Lucas, 1955; Nielsen, 1955). Knowledge of viruses as pathogens of marine fishes is even more rudimentary than is that for bacteria, except for tumor-inducing agents. Currently available established cell cultures of marine fish origin should do much to improve our understanding of viruses in the oceans.

XI. Summary

Diseases of marine fishes are less well known than those of fresh-water species because:

(*a*) Mortalities and epizootics in the sea are so much less apparent and less frequently observed than are those in the more restricted fresh-water habitat, that the true role of disease in the sea has not been fully appreciated.

(*b*) Fresh-water hatcheries and aquaria are much more numerous than comparable salt-water facilities. Problems associated with crowding, artificial feeding and disease control for salt-water species have not had to be confronted with the same intensity of research as for fresh-water species. Much of the impetus for research and the advances in understanding of disease in fresh-water fishes have originated in the hatchery or aquarium environment; this impetus has been largely lacking for marine species.

(*c*) The marine environment is less amenable to manipulation than is the fresh-water environment, and problems of disease control in the sea have seemed insurmountable to some people.

The widely-scattered world literature on marine fish diseases encompasses a body of knowledge that is growing rapidly with increasing scrutiny of the oceans and their inhabitants as actual and potential food sources for an expanding human population. The species of fishes studied are primarily members of commercially important groups such as gadoids and clupeoids, and attention has been paid to those conditions which affect survival or marketability. Diseases of marine fishes are important economically because they: (1) reduce the number of fish available to man; or (2) reduce the quality of fish as food. Important to (1) are epizootics and resultant mass mortalities caused by infectious agents. Less conspicuous but also important are " background " effects of disease that result in continuous direct or indirect subtraction of individuals from a population. Important to (2) are parasites that inhabit and sometimes degrade the muscles of marine fishes. Conspicuous in this group are the Microsporidea, Myxosporidea, larval worms and tissue-invading copepods.

Infectious diseases produce dramatic effects, such as epizootics and mass mortalities. Bacteria, fungi and protozoans have all been implicated in marine diseases of serious consequence. Severe short-term effects of outbreaks on population size and on commercial landings have been observed in Atlantic herring, white perch and other species. Repeated outbreaks of certain infectious diseases, such as red disease of eels and *Ichthyophonus* disease of herring, have been recorded.

Among the invasive diseases, larval cestodes, trematodes and nematodes can be found, often in large numbers, in the flesh and viscera of marine fishes, where they may interfere with metabolic activities and with growth, or they may otherwise reduce the value of the parasitized fish to man. Tissue-invading copepods may act in similar ways. Enzootic centers exist for certain parasites, for example larval nematodes and some copepods; occasionally parasites such as monogenetic trematodes increase in abundance locally to produce epizootics.

Abnormalities, including tumors and skeletal deformities, are known for many marine species. Most of the morphological variations, other than tumors, can probably be attributed to defects in embryonic development—in fact a wide range of abnormalities has been seen in larval fishes, especially those reared in environments in which oxygen, salinity, light or other factors deviated from normal.

Studies of captive marine fishes have provided much information about diseases. Many pathogens multiply rapidly in the aquarium environment to produce epizootics; other organisms, which may be insignificant in the natural habitat, may assume pathogenic roles. *Vibrio* infections are common in marine aquaria, and may quickly destroy captive populations. The dinoflagellate *Amyloodinium* and the ciliate *Cryptocaryon* have been causes of epizootics in marine aquaria, but, as far as it is known, are not significant pathogens in natural populations.

Gratifying recent increases in research on fish diseases indicate that we may soon be able to assess with some reliability the role of disease in marine species.

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LARVAL ECOLOGY OF THE TREMATODE *CRYPTOCOTYLE LINGUA*

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The life cycle of *Cryptocotyle lingua* in northern New England involves the periwinkle (*Littorina littorea*), the sea herring (*Clupea harengus*), and the gull (*Larus argentatus*). Ecological considerations implicit in such a complex sequence of hosts offer excellent research possibilities, particularly those concerning the relationship of larval *Cryptocotyle* to snail and herring populations. A long-term study of this parasite in the western North Atlantic has provided some information about interactions with hosts and with environment. Trematode invasion sterilized the snail host and inhibited host participation in seasonal migrations from the high-tide zone in autumn and to the high-tide zone in spring. Highest larval parasite incidences were consistently found in snail samples from the high-tide zone, particularly in winter, during a two year study. Differential movement of parasitized and normal snails was determined by marking experiments. Many parasitized snails were immobilized in the high-tide zone in late autumn, while most unparasitized snails retreated to dense aggregations below the mean low-tide line.

Seasonal variations in state of maturity of infections and in cercarial emergence were also noted. Cercarial emergence occurred only from May to December; this was also the period when schools of immature herring were common in inshore waters. During the winter months infections regressed, so that mature cercariae were absent — a phenomenon shown experimentally to be related to decreasing environmental temperature and in a limited way to light. Laboratory studies demonstrated that cercarial emergence declined with decreasing water temperatures and ceased at about 10 °C. Maturation of infections and emergence of cercariae were induced during winter months by maintaining parasitized snails for three weeks in sea water warmed to 16 °C. Experimental increase in day length to 16 hours during winter months did not enhance maturation or cercarial emergence, but maintenance of parasitized snails in constant light or constant darkness during the summer caused cessation of cercarial emergence and regression of infections. Environmental salinity below 18 parts per thousand also inhibited cercarial emergence.

Snail samples collected from the shores of the Gulf of Maine displayed marked variability in larval trematode incidences (from 0 to 82 per cent), but no general geographic changes in parasite abundance in this area of the western North Atlantic. However, incidences of *Cryptocotyle* metacercariae in the fish intermediate host decreased markedly from west to east in each of three years of sampling (1961-1963), possibly due to geographic changes in maximum inshore water temperatures. Summer water temperatures on the western coast of the Gulf of Maine usually exceeded 15 °C. while those on the eastern coast were generally below 10 °C. These findings, when combined with experimental results, suggest that environmental temperature may exert a severe limiting influence on parasite abundance in the area of study, and that the northern New England coast may be a marginal zone for the parasite because of temperature.

Cercarial invasion was found to have striking effects on immature herring. Samples, especially from the western Gulf of Maine, often included many individuals parasitized by several hundred *Cryptocotyle* metacercariae. Experimental studies, exposing herring of different age groups to specific cercarial densities, disclosed that mortalities could result from massive continuous invasions but not from massive short-term exposures. Younger age groups were killed more rapidly by cercarial invasion.

Here, then, is a larval parasite that reduces the reproductive potential of the first intermediate host and immobilizes it in an unfavorable life zone in winter; and may kill its second intermediate host if present in sufficient numbers. Environmental conditions favoring completion of the parasite life cycle exist principally in summer, when herring schools move inshore near concentrations of *Littorina*, at a time when, because of temperature, cercarial emergence is at a maximum. Although other factors may be involved, geographic variations in incidence of metacercariae seem related directly to summer environmental temperature in the Gulf of Maine, and temperature seems to be a critical factor in the ecology of larval *Cryptocotyle lingua*.

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PARASITES OF OYSTERS, *CRASSOSTREA VIRGINICA*, FROM THE EAST COAST OF NORTH AMERICA

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Widespread mortalities of American oysters, *Crassostrea virginica*, apparently of disease etiology, have occurred in some areas along the East Coast of North America within the past decade and have focused attention on diseases and parasites as factors important in the ecology of shellfish. At present a number of research and academic institutions in the United States and Canada are carrying on studies of oyster parasites, and knowledge is increasing slowly but persistently. This paper is based on results of continuing oyster disease research being conducted by the U. S. Bureau of Commercial Fisheries, and on published information from other research groups.

Probably the most refractory to understanding are pathogens thought responsible for epizootics leading to mortalities of oysters in the Gulf of Saint Lawrence and in the waters off the Middle Atlantic States of the United States. A protozoan parasite has been implicated in U. S. mortalities but its complete life cycle has not been elucidated nor has experimental transmission been effected. Largely because of these major gaps in knowledge, no scientific name has been proposed and no description of the parasite exists in the scientific literature. The life cycle stages that have been recognized are reminiscent of stages seen in the life cycles of haplosporidians, but a diagnostic spore stage has not been identified. However, epizootiological evidence suggests strongly that this organism — nicknamed MSX (multinucleate sphere of unknown taxonomic position) — is the pathogen responsible for recent mortalities. Its presence in dead and dying oysters, its absence from areas that have escaped mortalities, and its appearance in oysters transplanted into mortality areas, all point to its role as a significant oyster pathogen.

Another parasite, this time with fungal characteristics, has been definitely associated with mortalities of oysters on the Southern Atlantic and Gulf Coasts of United States. This pathogen is *Dermocystidium marinum*. First recognized and described as a parasite of oysters from the Gulf of Mexico, the organism is now known to occur as far up the Atlantic Coast as Delaware Bay. A recent survey of oyster parasites in more northern waters, using a diagnostic culture method, has not disclosed infections with *Dermocystidium*. The disease has been reported to cause significant levels of mortality in southern waters, and seems limited in its distribution by salinity and temperature. The fungus, like the haplosporidian discussed above, does not usually occur in salinity below 12 parts per thousand, and low environmental temperatures appear to retard its development in infected oysters.

Other parasites of American oysters have been recorded during a recent survey along the North American East Coast and reported in the literature. These include another haplosporidian, *Minchinia costalis*. Several life cycle stages of this protozoan parasite are similar to MSX, but a definitive operculate spore has been identified. Two gregarines of the genus *Nematopsis* occur in oysters. One of these, *Nematopsis ostrearum*, has been found in the recent coast wide survey to occur in as much as 100% of a sample. Cysts of this protozoan may occur with great abundance in individual oysters. A flagellate, *Hexamita inflata*, occurs sporadically in oysters, in greater abundance during the winter months. It has been variously described as a pathogen with intracellular parasitic stages or as a normally harmless inhabitant of the oyster that may increase in abundance during periods of reduced metabolism, such as would be produced by low environmental temperatures.. *Ancystrocoma*, a relatively common but probably non-pathogenic ciliate, has been observed in oyster samples from several areas. The parasite has not been found in abundance in individual hosts. Larval stages of the trematode, *Bucephalus cuculus*, occur in American oysters, usually with low incidence which varies seasonally and geographically. Infections reach a peak in summer. The cestode genus *Tylocephalum* is represented by encysted larvae in oysters sampled in Appalachicola Bay, Florida. Such larvae have not been found in samples taken north of Florida, except when oysters introduced into Chincoteague Bay, Virginia, from Florida were reexamined several months after introduction. A number of undescribed parasites have been observed during the recent survey, including larval nematodes and several unidentified fungi, one being morphologically similar to *Ichthyosporidium* found in marine teleosts.

In conclusion, a continuing investigation of shellfish diseases and mortalities carried on by the U.S. Bureau of Commercial Fisheries has included a survey of the distribution and abundance of oyster parasites on the East Coast of North America. This study has indicated the existence of geographic and seasonal variations in occurrence of known parasites. Protozoan and fungal parasites have been implicated in mortalities of oysters, and it seems likely that other pathogens will be recognized during long term studies now in progress. It is already apparent that disease is a significant factor in determining survival and abundance of oysters.

Long-Term Tags Field Tested

Scientists Explore The Problem Of Lobster Population Identity

By BERNARD E. SKUD
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The Bureau of Commercial Fisheries, an agency of the U.S. Dept. of Interior, is concerned and the management and conservation of marine fisheries. The Bureau works to assure that these renewable resources are fully developed and wisely used — contributing the most to the nation's progress and prosperity.

In Maine, the Bureau's research arm is headquartered at the Biological Laboratory in Boothbay Harbor. Studies are concentrated on two species — sardines and lobsters — but also include many facets of biological oceanography.

In the past three years, staff scientists have written some 50 papers on the results of their research. These articles have appeared in a variety of technical journals which are published by scientific societies and international organizations. Several popular accounts also have been written to inform the fishing industry and general public of the research progress.

The staff of the Biological Laboratory includes 30 trained scientists and technicians, and 15 supporting administrative and maintenance personnel. The scientists cooperate with many state and university scientists in New England and with foreign scientists in organizations such as the International North Atlantic Fisheries Commission.

The Laboratory is well equipped with modern facilities and includes an efficient sea water system used for experimental studies. Two vessels — one 40 feet and another 60 feet long — are permanently assigned to the Laboratory, and two larger vessels — 110 feet and 180 feet long — are utilized each spring and fall for research cruises on the high seas.

The Bureau's research on lobsters was initiated a year and a half ago and has attracted considerable attention. The recent tagging experiment on Monhegan Island is of particular interest to the local fishermen, but the study was designed to provide basic information which will be helpful in all lobster fisheries.

Purpose of the experiment is to test long-term tags which are retained by the lobsters during and after shedding. These tags have been successfully retained by lobsters in the Laboratory and now are being tried under field conditions for the first time. A reward of $2 is being paid for each tagged lobster that a fisherman captures and returns to the Laboratory. These tagged lobsters also will provide information on migrations and growth — data needed to adequately manage the fishery.

Lobsters were tagged with plastic tubing inserted in the "elbow" of the claw, or anchored in the muscles of the back between the body and tail Others were branded with an "X" on the back of the lobster.

In addition, some of the spiny projections on each side of the tail were removed. The missing tail-spines will take two or three years to grow back and will serve as a check on the effectiveness of the tags. Each tag was coded and labelled with the Bureau's initials (BCF).

The tagging experiment will help to determine the feasibility of tagging in offshore areas. Biologists must validate laboratory results which indicate that the new tags will be retained through shedding, that there is no serious injury to the tagged lobster, and that there is no effect on its behavior. The importance of these studies has been explained to the Monhegan fishermen and the success of the study is dependent on their cooperation.

MONHEGAN STUDY

The Monhegan study is a basic part of the federal program to study the relationship between "inshore" and "offshore" populations. Proper management of the lobster fisheries is dependent on the knowledge of whether or not these populations are discrete.

In addition to tagging studies, other approaches are being used to make this determination. The biochemical characteristics of lobster blood are being compared, using modern and sensitive techniques that reflect the genetic makeup of the animal. "Messmates" and "free loaders" such as barnacles and other organisms which are attached to the lobster's shell or exist internally can provide evidence on the lobster's origin.

This provides another approach to the problem of population identity which is being explored by Bureau scientists. Another method of comparing populations is to measure various body proportions of the lobsters. This phase of the research has been contracted to the Narragansett Marine Laboratory, University of Rhode Island, where computer processing will hasten data analyses.

Data on offshore lobsters are collected from Bureau research vessels — Delaware and Albatross IV. Three cruises were conducted last fall that ranged from Corsair Canyon on the northern part of the continental shelf to Hudson Canyon in the south. Samples collected from these vessels also provide general information about the lobster populations — for example, their size, and shedding and spawning time.

SCUBA DIVERS

Other aspects of lobster behavior are being studied through the techniques of scuba diving. Scuba diving has been used successfully in marine fisheries research before, but its use is somewhat limited when concerned with species of fish that are capable of moving rapidly from place to place.

Lobsters are particularly suitable subjects for such studies, since they live on the bottom and are easily located and handled by divers. The divers follow all of the safety procedures and requirements prescribed by the Navy, and are equipped with the latest in diving gear, including an underwater communication system.

This system allows the divers to converse with one another while diving, as well as with the personnel aboard the vessel. The purpose of these studies is to record precisely the habitat of lobsters at all stages of their life and to define the movements and behavior of the lobsters.

This information is needed and will be used to plan and execute tagging experiments. Lobsters will be tagged or marked and released in particular study areas and observations from diving, as well as recoveries by fishermen, will provide information about lobster biology and the lobster fishery.

KNOWLEDGE EXCHANGED

The Bureau is coordinating its activities with the efforts of other agencies conducting lobster research, and recently held a meeting of some 30 scientists working in this field. Representatives were from the Fisheries Research Board of Canada, Newfoundland, Quebec and St. Andrews; Maine Department of Sea and Shore Fisheries; University of New Hampshire; Massachusetts Division of Marine Fisheries; University of Rhode Island; New York Department of Conservation; and the Connecticut Board of Fisheries and Game.

The meeting provided a direct exchange of knowledge among all persons engaged in lobster biology and management. Special emphasis was placed on the relationship of inshore and offshore lobsters, on ways of increasing lobster supplies through habitat improvement, and on methods for studying lobster migration.

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Size composition, sex ratio and maturity of offshore lobsters. (By title only.)

Over 4,000 lobsters (*Homarus americanus*) from Georges Bank and adjacent areas of the continental shelf were measured and sexed by the U. S. Bureau of Commercial Fisheries during the past decade. The lobsters were taken in depths to 400 fathoms by research and commercial fishing vessels. The carapace length ranged from 5 to 21 cm and the weight from 0.2 to 13.0 kg. Mean length from the research cruises averaged 13 cm and mean weight almost 3 kg. In contrast, lobsters from the inshore fishery average about 9 cm and weigh less than 1 kg.

Over 60% of the offshore lobsters were females; their dominance was greatest during the winter. The sex ratio of lobsters between 5-7 cm was 1:1. The ratio of females increased with size, accounting for 70% in some samples of large lobsters (14-16 cm). Above 17 cm, the dominance of females decreased, and between 19-21 cm males were in greater abundance. The carapace length of the smallest egg-bearing females was 9 cm. Between 12 and 17 cm, 50% of the females were egg-bearing in some of the summer and autumn samples. Relatively few lobsters over 18 cm were egg-bearers.

The seasonal variation in sex ratio and the dominance of females probably reflects changes in behavioral patterns which influence catchability, sexual differences in molting rate after maturity, and the effects of regulations requiring the release of egg-bearing females.

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LAMPREY CONTROL AND RESEARCH IN THE UNITED STATES

by

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Sea lamprey control progressed well in 1964 despite severe drought conditions in the Great Lakes region. Low flow in streams delayed many scheduled treatments, but made possible a relatively economical treatment of the Muskegon River, one of the largest tributaries of Lake Michigan. Fifty-two streams discharging 6,552 cfs of water were treated with 118,840 pounds of lampricide (Table 1).

Table 1. Summary of chemical treatments in United States waters of the Great Lakes in 1964.

	Number of streams	Discharge at mouth (cfs)	Stream miles treated	Lampricide (pounds)	Synergist (pounds)
Superior[1]	25	1,637	259	18,255	113
Michigan[2]	27	4,915	1,522	100,585	212
Total	52	6,552	1,781	118,840	325

[1] Includes 17 re-treatments

[2] Includes 12 re-treatments

No significant change in the number of spawning-run sea lampreys occurred in Lake Superior; 11,969 lampreys were taken at the electric barriers compared on 11,111 in 1963. The Brule River run accounted for more than half (56.2 percent) of this total. Stream surveys, fyke net fishing, and trawling continued to indicate a general reduction in the ammocete population in streams on the south shore of Lake Superior.

Investigations of the persistence of the lampricide in streams and its effect on aquatic life were continued.

Lake Superior surveys

Thirty-two Lake Superior tributaries were surveyed in preparation for chemical treatment or to determine the distribution of re-established populations. An intensive survey of the upper Brule River found 2 transforming sea lampreys above the 1962 chemical application point. Continued examination of oxbow ponds and other backwater areas on the Ontonagon River and the Sturgeon River, revealed no isolated ammocete populations.

Re-surveys of 46 marginal streams found sea lamprey ammocetes for the first time in Reefer Creek, Bayfield County, Wisconsin. Since the size, turbidity, and depth of the lower St. Louis River in Minnesota made standard survey techniques unreliable, sea lamprey ammocetes were placed in cages in the river in midsummer to see if conditions were suitable. Dissolved oxygen content of the river dropped to 0.0 ppm, water temperatures reached the low 80's during this period, and all ammocetes died within 6 weeks. Sea lamprey spawning activity in Minnesota streams appeared to be about half that of 1963. Only the Split Rock River had more than a few nests or adults. Two streams in Wisconsin, however, were heavily used. More than 80 nests were found just above the Brule River barrier after it was shut down in mid-July. Several hundred nests were seen in the Bad River and 3 of its tributaries.

Posttreatment surveys were completed on 24 streams. Residual populations of ammocetes were located in the Ontonagon River, Furnace Creek, and McCallum Creek. Reestablished populations were found in Seven Mile Creek, Beaver Lake Creek, and Mosquito River. All other streams were negative.

Lake Superior chemical treatments

Chemical treatment of streams along the south shore of Lake Superior began on April 29. Optimum conditions for treatment continued until the last week in July when low flows were encountered. Only 1 stream was treated in August, but in September and October increased rainfall improved the situation and 13 streams were treated.

Twenty-five streams with a total discharge of 1,637 cfs were treated (Table 2). Of these, 21 were treated with TFM and the remaining 4 with a synergistic mixture, (TFM-2B), containing 98 percent by weight of TFM and 2 percent 5,2'-dichloro-4'-nitrosalicylanilide (Bayer-73). Eight streams treated for the first time contained small ammocete populations in the lower stretches. Survivors from previous treatments were not found in significant numbers in any of the 17 re-treatments. The Bad River, Ashland County, Wisconsin, was re-treated to eliminate residual ammocetes which were most abundant in one of its larger tributaries, the Potato River. Fifty-seven residual sea lamprey larvae, 2 recently transformed individuals, and many young-of-the-year larvae were recovered from the Potato River while in the other tributaries, 13 residual larvae, 1 transformed sea lamprey, and many young-of-the-year larvae were collected. The accuracy of the survey of the residual population prior to treatment was substantiated by these collections.

There was no serious fish kills during the 1964 treatments.

Lake Michigan surveys and bioassays

Re-examination of 19 potential lamprey-producing streams disclosed no new population. Surveys were completed on 29 streams scheduled for re-treatments. The distribution of ammocetes was unchanged in 14 streams, extended in 1, and reduced in 9. Five streams had no re-established larvae present. Pretreatment checks also were made on 3 large streams surveyed in 1961. Distribution limits were unchanged at 22 of 24 locations investigated. Posttreatment surveys were finished on 29 streams. Small numbers of residual sea lampreys were found in the Boardman, Crystal, Big Manistee, Pere Marquette, Pentwater, Pensaukee, Big Cedar, Ford, and Black Rivers.

In 1964, 63 bioassays were completed on 28 Lake Michigan tributaries. Of this total, 47 assays were run with TFM, 13 with TFM-2B, and 3 with TFM-1B.* All bioassays used rainbow trout as test fish except for the main Muskegon River where simultaneous assays were run with rainbow trout and brown trout. Several native species, (34 brown trout, 6 white suckers, 15 sculpin, 5 northern creek chubs, 1 hog sucker, 1 rock bass, 3 northern pike, 11 common shiners, and 3 brook trout) survived the selected concentration for 12 hours in a continuous-flow test utilizing one trough of the mobile bioassay laboratory. The subsequent successful treatment of the Muskegon River, with minimal loss of fish, confirmed the results of the assay.

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[*] Synergistic mixture containing 99 percent TFM by weight and 1 percent Bayer-73.

Table 2 -- Details on the application of lampricide to tributaries of Lake Superior in 1964.

Stream	Date	Discharge at mouth (cfs)	Concentration (ppm)		TFM (pounds)	Synergist (pounds)
			Minimum effective	Maximum allowable		
Furnace Creek	April 29	33	2.0	5.0	240	....
Buck Bay Creek[1]	May 5	15	2.5	9.0	162	....
Cranberry River	May 8	59	1.5	3.0	180	....
Traverse River	May 14	53	0.7	2.0	204	....
Smith Creek[2]	May 15	9	3.0	5.0	90	....
Mud Lake Outlet[2]	May 16	50	0.8	1.3	162	....
Union River[2]	May 17	11	2.5	4.0	72	....
Potato River	May 18	40	2.0	4.0	558	....
Little Iron River[2]	May 18	40	2.0	5.0	234	....
Tahquamenon River	July 15	290	2.0	5.0	3,330	88.5
Garlic River	July 23	12	2.5	6.0	162	....
Sand River	Aug. 26	50	2.0	7.0	936	....
Munising Falls Creek[2]	Sept. 3	2	5.0	10.0	18	....
Firesteel River	Sept. 10	73	1.5	3.5	414	11.5
Elm River	Sept. 10	15	1.5	4.0	99	2.5
Ravine River	Sept. 22	20	2.0	4.5	180	....
Slate River	Sept. 23	7	2.5	5.5	54	....
Falls River	Sept. 24	100	1.7	5.0	378	10.5
Bad River	Oct. 4	560	2.5	7.0	8,982	....
Reefer Creek[2]	Oct. 15	4	6.0	13.0	216	....
Fish Creek (Orienta)[2]	Oct. 16	1	3.0	8.0	108	....
Sand River[2]	Oct. 16	5	4.5	11.0	306	....
Arrowhead River	Oct. 19	150	1.0	1.5	594	....
Split Rock River	Oct. 19	13	2.0	4.0	162	....
Waiska River	Oct. 28	25	2.0	5.5	414	....
TOTAL		1,637	....	....	18,255	113.0

[1] Au Train River tributary treated to keep ammocetes from reaching Au Train Lake.

[2] Initial treatment.

Lake Michigan chemical treatments

Chemical treatments on Lake Michigan streams began in mid-April and ended in late October. Summer treatments were again handicapped by low flow in many streams. A rapid reduction in flow halted the Cedar River treatment in June with only the upper two-thirds of the river completed. Treatment of the lower one-third of the river was finished in August.

Twenty-seven streams with a total discharge of 4,915 cfs were chemically treated (Table 3). Fifteen streams received initial treatments and 12 were re-treatments. Sea lamprey larvae were noticeably less abundant in re-treated streams.

Eleven streams were treated partially or completely with the synergistic mixture TFM-2B. Maintaining a homogeneous suspension with the 2-percent synergistic mixture in TFM and pumping this mixture in precise amounts continued to be a problem in 1964. New techniques were tried experimentally in 1964, but results were no better. Appreciable mortality of brown and rainbow trout during the treatment of Pentwater River discouraged regular use of the mixture for the remainder of the season.

Three assays and 1 chemical treatment were conducted using the TFM-1B formulation. The treatment appears successful, but bioassay results indicated the necessity for more testing of this formulation.

Lake Huron surveys

The continuing survey of the St. Marys River in 1964 showed that sea lamprey ammocetes were present in the main river upstream as far as the U. S. locks, but were absent from its tributaries above Munuscong Lake. No adults or nests were observed in areas of apparently suitable habitat.

Electric barrier operations

Electric barriers were operated from April 1 to July 13 on 22 streams along the south shore of Lake Superior. The only problem encountered throughout the season was flood damage to the barrier on the Firesteel River which required extensive repairs.

The assessment barriers captured 11,969 sea lampreys (Table 4), 858 more than in 1963, 2,847 more than in 1962, but 55,261 less than in 1961. The catch is 79 percent below the 5-year average, 1957-61, before control measures became effective.

Table 3 -- Details on the application of lampricide to tributaries of Lake Michigan in 1964.

Stream	Date	Discharge at mouth (cfs)	Concentration (ppm) Minimum effective	Concentration (ppm) Maximum allowable	TFM (pounds)	Synergist (pounds)
Pentwater River[1]	April 16	93	2.0	6.0	1,044	14.5
Ahnapee River[1]	April 17	14	7.0	17.0	432	...
Three Mile Creek[1]	April 19	3	3.0	7.0	40	1.0
Pensaukee River[1]	April 21	20	3.0	7.0	288	8.0
Lincoln River[1]	May 8	107	4.0	12.0	1,815	...
Pere Marquette River[1]	May 25	572	5.0	16.0	19,620	...
Manistee River[1]	June 4	1,844	6.0	13.5	31,392	...
Ford River[1]	June 15	330	5.0	14.5	12,294	45.5
Arthur Bay Creek[1]	June 28	2	6.5	16.0	18	...
Johnson Creek	July 9	1	3.0	9.0	6	...
Poodle Pete Creek	July 10	2	2.0	5.0	27	...
Parent Creek	July 10	5	2.5	7.5	36	1.0
Gulliver Lake Outlet	July 13	3	5.0	10.0	72	...
Bulldog Creek	July 13	6	2.0	5.0	108	3.0
Millecoquins River	July 23	71	9.0	20.0	1,314	21.5
Mile Creek	Aug. 5	1	2.5	6.5	9	...
Black River	Aug. 5	13	5.0	12.0	333	...
Paquin Creek	Aug. 9	13	6.0	10.0	168	...
Brevort River	Aug. 9	5	5.0	10.0	99	...
Big Cedar River[1]	Aug. 12	170	3.5	8.0	5,004	56.5
Boyne River	Aug. 26	80	6.5	8.5	1,710	47.5
Yuba Creek	Aug. 30	3	8.0	18.0	54	...
Big Bear Creek[1]	Sept. 12	12	3.0	7.0	126	2.0
Muskegon River[1]	Sept. 15	1,485	6.0	15.0	23,454	11.5
Black Creek[1]	Oct. 15	43	5.0	12.0	684	...
Pigeon River	Oct. 18	11	4.0	13.0	306	...
Pine Creek[1]	Oct. 19	6	5.0	17.0	132	...
Total		4,915	...	...	100,585	212.0

[1] Initial treatment

Table 4 -- Catches of adult sea lampreys for comparable periods from 22 Lake Superior streams, and from 3 Lake Michigan streams, 1959-1964.

Stream	1959	1960	1961	1962	1963	1964
Lake Superior						
Waiska River	42	122	87	10	34	47
Pendills Creek	38	30	74	10	11	3
Betsy Creek	999	696	1,366	316	444	272
Two Hearted River	3,950	4,290	7,498	1,757	2,447	1,425
Sucker River	2,436	4,683	3,209	474	698	386
Hurricane River	63	80	96	6	36	31
Miners River	127	399	220	64	107	74
Furnace Creek	350	2,211	1,012	132	142	93
Au Train River	164	74	181	179	130	84
Rock River	1,170	2,598	3,660	399	353	229
Chocolay River	3,486	4,173	4,201	423	358	445
Harlow Creek	15	10	22	89	28	38
Iron River	250	317	2,430	1,161	110	178
Pine River	39	28	70	2	20	0
Huron River	1,408	1,237	4,825	70	201	363
Silver River	753	1,271	5,051	267	760	592
Sturgeon River	539	161	427	397	1,437	375
Misery River	2,433	696	962	80	24	12
Firesteel River	2,044	250	1,118	70	178	327
Brule River	19,156	9,539	22,478	2,026	3,414	6,718
Middle River	3,598	2,815	3,502	311	48	45
Amnicon River	968	1,094	4,741	879	131	232
TOTAL	44,028	36,774	67,230	9,122	11,111	11,969
Percentage change		-16.5	82.8	-86.4	21.8	7.7
Lake Michigan						
Sturgeon River	733	910	2,378	1,650	751	823
Bark River	1,047	1,065	1,085	710	298	202
Cedar River	6,856	4,676	9,423	5,729	6,412	3,568
TOTAL	8,636	6,651	12,886	8,089	7,461	4,593
Percentage change		-23.0	93.7	-37.2	-7.8	-38.4

The spawning run was one of the earliest encountered on Lake Superior. The first adults were taken during the week of April 11. The run increased rapidly and peaked during a 10-day period from May 16 to 25 when 36 percent of the total run was captured.

The number of sea lampreys from the 17 barriers east of Keweenaw Peninsula declined 37 percent compared to 1963. The catch from the western streams, however, increased 93 percent over the previous year. Much of this increase occurred in the Brule River. Its catch nearly doubled and accounted for 56.2 percent of the total for all the barriers. Only 2 rivers, the Brule and the Two Hearted, produced more than 1,000 sea lampreys in 1964 as compared to 13 in 1961.

The 3 index barriers on streams tributary to northern Green Bay, Lake Michigan, were installed April 7 and operated to July 2. The spawning runs increased erratically with a minor peak occurring between May 6 and 10 when nearly 18 percent of the total catch was made. A major peak occurred between May 21 and 25 which produced slightly more than 32 percent, and a minor peak, between June 5 and 9, accounted for 13.3 percent of the total catch.

The 3 barriers captured 4,593 spawning migrants compared to 7,461 in 1963, 8,089 in 1962, and 12,886 in 1961. This is the third consecutive year that the catch at these barriers has declined. The most significant reduction occurred at the Cedar River which produced 78 percent of the total catch. Its barrier captured 3,568 adults in 1964 compared to 6,412 in 1963, a decline of 44 percent.

The electric barrier on the Pere Marquette River on the east shore of Lake Michigan, which had not been operated since 1958, was reactivated April 1. The spawning run developed rapidly and by May 10, over 86 percent of the total catch had been taken. The total catch was 678 adults compared to 2,006 in 1958. An electric barrier on the Ocqueoc River, which is now being operated on Lake Huron as an index device took 2,677 adult sea lampreys compared to 4,674 in 1963.

There has been no significant change during the past 3 years in the size of sea lampreys taken from 11 Lake Superior streams. Their average length has remained at 16.6 inches and weight 5.5 ounces. No difference in size was discernible between sea lampreys in streams of eastern and western Lake Superior, however, a significant reduction in the sex ratio was recorded. The percentage of males dropped from 67.1 in 1963 to 54.8 in 1964. Only in the most eastern streams did the percentage of males (63.0) remain high.

Spawning migrants from the Bark River, Green Bay, Lake Michigan, were the smallest since 1957, averaging 15.9 inches in length and 4.3 ounces in weight. The percentage of males, however, was the highest (70.3), while the total number of sea lampreys captured was the lowest. Sea lampreys taken at the barrier on the Pere Marquette River were small also. Their average length and weight were 15.7 inches and 4.3 ounces. The run contained 60.3 percent males.

Spawning migrants entering the Ocqueoc River from Lake Huron had an average length of 15.8 inches. Although comparable to Lake Michigan adults in length, their average weight (4.7 ounces) was 0.4 ounce greater. Only 54.5 percent of the adults were males.

Only 877 spawning-run rainbow trout were counted at the barriers on Lake Superior compared to 1,390 for the previous year. Numbers of white suckers, however, increased over the catch in 1963. The incidence of sea lamprey wounds on rainbow trout increased to 3.5 percent from a low in 1963 of 2.2 percent. Nine and one-half percent of the Pere Marquette River (Lake Michigan) rainbow trout run and 23.3 percent of the Ocqueoc River (Lake Huron) run were scarred.

Movement of tagged sea lampreys from the St. Marys River

The tagging operation to determine the movements of adult sea lampreys congretated below the locks in the St. Marys River was repeated. A total of 403 lampreys was captured and tagged as compared with 159 in 1963. None of the 1963 group was taken at electric barriers, but 5 were reported by commercial fishermen. Of these, 2 were caught in gill nets off Gros Cap in Whitefish Bay, Lake Superior; 2 were taken in Lake Huron; and 1 was recovered in Lake Erie near Leamington, Ontario. Thus far, 6 of the 403 adults tagged in the fall of 1964 have been recovered. One individual, tagged October 25, was taken 12 days later near Gros Cap in Whitefish Bay. The remaining 5 recoveries have been from Lake Huron.

Fyke net operations

The fishing of fyke nets in tributary streams was continued during 1964 to monitor downstream movement of larvae and young sea lampreys. Fishing in 14 Lake Superior streams amounted to 1,415 net days and produced only 18 ammocetes. Nets were fished at the same time in 5 treated and 2 untreated streams tributary to Lake Michigan. Nets in the treated streams captured 13 recently metamorphosed lampreys; those in the 2 untreated streams caught 92 juveniles and 20 ammocetes. Unfortunately, spring fyke netting is carried on during a period when extreme fluctuations in water flows and heavy demands upon personnel maintaining barriers does not permit systematic operations required to provide comparable data from year to year.

Fyke nets fished as systematically as possible in 7 Lake Superior streams over several years during the more favorable fall season have demonstrated a substantial reduction in recruitment. A total of only 4 newly metamorphosed adults was captured in 1964 compared to 53 in 1961, representing a decline of 92.5 percent. A significant reduction in the production of young adults after initial treatments was revealed also by nets fished in 6 tributaries to northern Lake Michigan. In 1961, prior to chemical treatment, fyke nets in 5 streams captured 1,729 downstream migrants compared to 85 individuals in 1964 representing a reduction of 95.1 percent. In the remaining stream, the Ogontz River which was treated in 1960, only 5 young adults have been captured by the nets in 3 years of fishing.

Nets fished in several other tributaries to Lake Superior took 88 juvenile sea lampreys from the Brule River, 93 from the Sturgeon River, 7 from the Huron River, and 1 from the Silver River. Eighty-three of the 88 individuals taken in the Brule were captured in nets fished at a new location below a lake and above the chemical application site to pinpoint a source of contamination. Nets fished near the mouth of the stream in a manner comparable to the preceding years took 5 sea lampreys compared to 10 in 1963.

Fyke nets were fished in 6 streams (5 of them treated) along the east shore of Lake Michigan. Nets in the untreated White River captured 43 newly metamorphosed adults. Only 2 sea lampreys were taken from the 5 treated streams.

A fyke net has been operated continuously on the Ocqueoc River for 2 years. Accurate catch records of invertebrates, fish, and lampreys are being kept to compare with data obtained following chemical treatment of this stream. The 1963-64 downstream movement of sea lampreys began on November 6, and ended May 15, 1964. The net captured 3,373 recently transformed sea lampreys. The peak movement occurred between March 6 and April 24 when 2,509 individuals or 74 percent of the catch was made. A total of 626 young juveniles, nearly 19 percent of the catch, was captured between November 12 and

December 26, 1963. The 1964-65 downstream movement in the Ocqueoc River began November 3, very close to the starting date in 1963. The fall peak also closely coincided with that of the preceding year. The catch between November 9 and December 17 numbered 920 individuals as compared to 626 for the preceding year.

The large number of recently transformed lampreys in the Ocqueoc has provided the opportunity to measure the net's efficiency through a mark and recovery study. Based on recovery data from 1,320 marked individuals, the estimated production of the Ocqueoc River for the 1963-64 season is 42,000 sea lampreys.

The mechanical screen on a water intake of a chemical plant near the mouth of the Pere Marquette River was used again in 1964 as a collecting device for recently metamorphosed sea lampreys. Collections from the screen vividly illustrate the reduced production of young adults following an initial treatment with the larvicide in May 1964. The number collected during the following November dropped to 0.27 per day compared to 523.30 in 1963, a 99.97-percent reduction.

Re-establishment in treated streams

The study of larval sea lamprey populations which have become established in streams following chemical treatment was continued. No evidence of transformation was found among 4-year-old larvae in 7 streams under special study since 1960. The 1960 and 1961 year classes of larvae were present in 72 of the 77 infested Lake Superior streams. However, a significant reduction in the number of repopulated streams has occured in the last 3 years. No re-established populations have been found during this period in 26 streams and 19 streams contain only small numbers of a single year class. To date, the 1964 year class has been detected in 17 streams. Failure of sea lampreys to re-establish themselves in many of the streams may be due to a reduced spawning population, effective operation of the assessment barriers, chemical treatments during the spawning period, and adverse environmental conditions. Collections from the study streams indicate that changes take place in ammocete distribution.

The electric beam trawl was used extensively during 1964 along the north and east shores of Lake Michigan in the search for lake-dwelling ammocetes. The extremely low lake level limited the amount of coverage at several promising areas.

Over 31 hours of trawling at 22 locations produced only 13 sea lamprey ammocetes. They were captured May 19, off the mouth of Ford River. Trawling in deeper water off the Ford River failed to take sea lampreys. Native lampreys also were scarce in areas along the north shore. Only 12 were captured; 10 were taken off the mouth of Ford River, 1 off the Cedar River, and another near the mouth of the Fishdam River.

Trawling in areas along the east shore was even less productive. Only 17 ammocetes of all species were taken in nearly 29 hours. The catch contained 3 sea lampreys; 2 from the south arm of Lake Charlevoix and 1 from the east arm of Traverse Bay. Native lampreys were caught at 5 locations for the most part in the south arm of Lake Charlevoix.

Trawling in Lake Superior was limited to resurveys of potential problem areas east of the Keweenaw Peninsula. A total of 11 sea lamprey ammocetes was captured in 3 of the 12 areas examined. Of the 11 larvae, 9 were taken in Furnace Bay, 1 in Portage Canal near the mouth of the Sturgeon River, and 1 from East Bay of the Sucker River. The trawl also captured 47 native ammocetes. These were taken from 6 different locations. The lake dwelling populations found in both Lake Superior and Lake Michigan are considered small.

Sea lamprey research

Development of more effective and less costly lampricides continues to be the dominant research activity. Studies of factors affecting the activity of 3'-chloro-3-nitrosalicylanilide (33NCS), elucidation of the relationships between molecular structure and biological activity in salicylanilides, and some screening of unrelated compounds were the major features of the chemical research program.

Biological studies have been concerned with the effect of environmental influences on larval growth, attempts to raise larval lampreys of known parentage for life-history and taxonomic study, and effects of TFM on fish-food organisms.

Development of 33NCS. Evaluation of the relationship of molecular structure to biological activity in the salicylanilides resulted in the selection of the chemical 3'-chloro-3-nitrosalicylanilide (33NCS) for further development since it could be easily and economically synthesized.

A series of bioassays conducted in waters from 8 different sources in the Lake Huron and Lake Michigan drainages indicated that 33NCS is affected by water quality in much the same way as TFM. However, the selective action persisted even when relatively large amounts of the compound were required because of increasing water hardness. The action of 33NCS in simulated stream tests in flowing water raceways was not as encouraging. Although toxicity to fish remained the same, the minimum lethal concentration for larval lampreys was 0.6 ppm or almost twice that established from laboratory studies. The range of concentrations in which the compound could be used selectively was, therefore, reduced.

The reasons for the difference between laboratory and simulated stream tests results are not known. Difficulties in formulating and feeding 33NCS and analyzing for concentration may have produced variations. Improved formulations of 33NCS and better analytical techniques should allow a more effective evaluation of future raceway testing. A dye complexation technique has been developed which will permit accurate determination of concentration to at least 0.05 ppm.

Screening of new chemical compounds. Forty-seven new compounds were tested; of these, 20 were nontoxic to larval lampreys at 10.0 ppm and 27 were toxic at 10.0 ppm or less. Further testing indicated that 14 of the 27 were selectively toxic to larval lampreys.

Larval growth and transformation. It has been found that nutritional levels can affect larval transformation as well as growth. Studies are presently underway to relate these findings to other environmental factors such as temperature. Ammocetes of known age are being maintained under various programs of food and temperature regulation.

Larvae of known parentage. Identification of young-of-the-year larvae and separation of the 3 species in the Genus *Ichthyomyzon* are difficult. In an attempt to find distinguishing features, ammocetes of known parentage are being reared in the laboratory and embryological development of each species followed. Large numbers of stage 17 (burrowing) prolarvae, 29 days from fertilization, have been preserved and are being examined.

Effects of TFM on fish-food organisms. Mortality of some aquatic invertebrates and unusual emergence of some insect species during chemical treatments prompted a study of the effects of TFM on fish-food organisms. Square-foot bottom samples have been taken on several streams immediately prior to chemical treatment, 1 week after treatment, 6 weeks after treatment, and 1 year after treatment. Similar samples have been taken from untreated streams carefully selected to provide comparable data.

Generally, representatives of all the major orders of aquatic insects except Odonata show a slight reduction in numbers immediately after chemical treatment. The greatest decline occurs among members of the order Trichoptera and Coleoptera, while smaller reductions generally take place among Diptera, Hemiptera, and Ephemeroptera. Recovery is usually rapid, with most groups returning to their pretreatment numbers within 6 weeks. All groups in streams treated prior to and during 1963 have shown a complete recovery.

TFM residues in the environment. Further development of methods to recover TFM from fish and natural waters utilizing acid hydrolyzation, solvent extraction, and ion-exchange resins, has led to a publication.*

Using these methods it has been found that fish exposed to the lampricide at low concentrations (2-4ppm) for periods ranging from 1 to 7 days and fish killed by higher concentrations contain no detectable TFM. Since it is possible that enzymatic degradation continues after death, fish are being analyzed immediately.

Samples of fish, food organisms, water, and sediments were collected from the Pentwater River, which was treated in the spring of 1963. Analysis of fish and water samples has shown no lampricide residue.

A new method of analysis for the characteristic groups attached to the benzene ring in the basic TFM structure with an infrared recording spectrophotometer has also been developed. The applicability of the technique is limited, however, because of the quantity of TFM needed in the sample for detection. A method to fractionate TFM into the pure substance, its isomers, and other impurities, by gradient elution chromatography also has been developed.

Water analysis. The first phase of a study of water quality of tributaries to Lakes Superior and Michigan was completed. From December 1962 through December 1964, analysis of stream waters were made at 136 stations on 99 tributaries of Lake Superior and 83 stations on 56 tributaries of Lake Michigan. Information on their conductivity, pH, alkalinity, hardness, concentration of calcium, magnesium, aluminum, copper, iron, chlorides, phosphates, nitrate-nitrite nitrogen, silica, sulfates, and tannin-and lignin-like compounds will be published shortly.

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* Daniels, Stacy L., Lloyd L. Kempe, Thomas J. Billy, and Alfred M. Beeton. 1965. Detection and measurement of organic lampricide residues. Great Lakes Fish. Comm. Tech. Rep. No. 9, 18 pp.

Experimental population of ammocetes. A single year class of sea lamprey ammocetes was established in the Garlic River in 1960. The population is isolated by a dam which blocks the upstream migration of spawning adults from Lake Superior. A downstream trap prevents the ammocetes from leaving the study area.

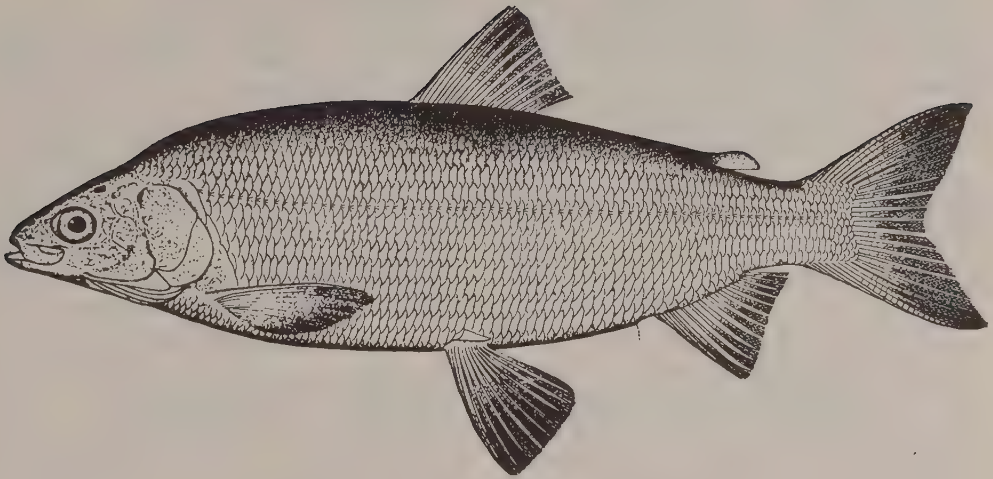
Collections taken each October from this population show a significant reduction in the rate of growth during the past 2 years (Table 5).

Table 5 -- Growth of 1960 year class of ammocetes in the Garlic River to October, 1964.

Year	Mean length	Length range	Length increment
1960	13mm	10-19mm	13mm
1961	39mm	25-54mm	26mm
1962	63mm	37-107mm	24mm
1963	80mm	52-134mm	17mm
1964	94mm	43-159mm	14mm

A substantial increase in the movement of ammocetes into the downstream trap occurred during the past year. A total of 2,847 individuals was captured in 1964 as compared to 379 in 1963. The period of major downstream drift extended from April through June.

Thus far, 3,314 ammocetes have been marked and returned to the study area. These include 318 individuals from the annual collection in October 1962, 700 in 1963, 400 in 1964, and 1,896 ammocetes captured on the downstream trap. A combination of colors and location of the marks permits the animals to be separated on the basis of time and point of release. During the 1964 collections, 59 marked ammocetes were recovered. These include 1 individual marked in October 1962, 13 marked in 1963, and 45 from the group taken at the trap in the spring of 1964. The marked ammocetes were collected within a half mile of their release. Thus far, there has been no evidence of metamorphosis.



THE TULLIBEE

STANFORD H. SMITH

Early explorers and settlers of the northeastern United States and southern Canada found lakes teeming with fish that had white flesh and were good to eat. The larger of these they called whitefish, differentiating two kinds — the lake whitefish and the round or menominee whitefish. These looked much alike, and each had the same appearance wherever it was found. The smaller fishes with white flesh had a variety of shapes, sizes, and colors in different lakes and areas, and were given several names; most common of these were "cisco," "lake herring," and "tullibee." Cisco subsequently became the common name for all of the small whitefishes, and lake herring was the name given to a single shallow-water species.

The use of the name "tullibee" became less common after ichthyologists concluded that it was a form of lake herring. The word recently assumed new importance, however, when one of our new atomic powered submarines was named "Tullibee" — an event that stimulated new interest in the word, its origin, and use.

"Tullibee" was first used in scientific literature by a noted British naturalist, Sir John Richardson, when he described a new species of fish taken from Pine Lake near Lake Winnipeg, and named it *Salmo* (*Coregonus*) *tullibee*. This fish was collected during the winter of 1819-20 by an expedition led by Captain Sir John Franklin into the Canadian Territory "to explore the northland." The Indians of the area called the

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fish otonabi — a combination of the Cree-Chippewa words "oton" meaning mouth, and "abi" meaning water. Anthropologists tell us that this name cannot be interpreted to mean that the fish were a delicacy that caused the Indians' mouths to water. They believe, instead, that the name refers to watery flesh or to lack of taste. Indeed, most of the ciscoes as we know them today have watery flesh and are frequently smoked to give them flavor. Epicures do not, however, consider the ciscoes tasteless. They sense a delicate and highly pleasing flavor that might be missed by others who are accustomed to well-seasoned food, or who consider fish only as sustenance, as did the Indians.

The French-Canadian explorers used these fish as food, but the name otonabi evolved into toulibi in their language. As the English settlers moved into the area the name was anglicized to tulibee and finally, tullibee.

In his description of tullibee, Sir John Richardson foretold the things that would cause it to lose its scientific standing. He observed that although the various species were different, description of the differences was so difficult that a person who had not seen a species could probably not identify it from a description. Ichthyologists eventually realized that the different enviornmental conditions of various lakes could make ciscoes look different although they were, in fact, the same species. Thus they learned that the tullibee was a variant of the lake herring — the most variable and widespread of the ciscoes.

As new information about the whitefishes and ciscoes brought greater understanding, the tullibee was known in the scientific literature at various times as *Coregonus tullibee, Argyrosomus tullibee, Leucichthys tullibee,* and *Leucichthys artedi tullibee.* In recent years the *tullibee* was dropped, and the fish that were recognized as tullibee are now referred to as *Coregonus* (*Leucichthys*) *artedi,* or just plain *Leucichthys artedi.* Formal recognition of the tullibee as a common name is now limited to the nipigon tullibee — a little-known species of cisco (*Leucichthys nipigon*) of uncertain status by modern taxonomic standards, found only in a few lakes of south central Canada including Lake Nipigon.

The tullibee was but one of many species of ciscoes described by ichthyologists that were later synonymized with the lake herring. Five species of ciscoes were described from Lake Erie during the early 1900's that were later considered forms of lake herring, and their names are now all but forgotten. The common use of tullibee has not changed, however, despite the manipulations of scientists. The residents of northern Minnesota and the adjacent region of southern Canada still use it for a certain type of cisco — a deep bodied form with bland, watery flesh that the Indians called, and may still call, otonabi.

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GALEUS PIPERATUS, A NEW SHARK OF THE FAMILY SCYLIORHINIDAE FROM THE GULF OF CALIFORNIA

By STEWART SPRINGER AND MARY H. WAGNER

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GALEUS PIPERATUS, A NEW SHARK OF THE FAMILY SCYLIORHINIDAE FROM THE GULF OF CALIFORNIA

By STEWART SPRINGER[1] AND MARY H. WAGNER[2]

ABSTRACT: Three specimens trawled from a depth of approximately 275 m. midway between Tiburon and Angel de la Guardia Islands in the Gulf of California, the only known specimens of the genus Galeus from the eastern Pacific, constitute the type series of a new species which is described and illustrated.

Among specimens collected at Station No. 64A2-16 of the R/V *Alaska,* operated by the California Department of Fish and Game, were five small sharks. Two of these were lost or misplaced but the collectors, John E. Fitch and Robert J. Lavenberg, sent us the three remaining specimens for study. These sharks, the first of the genus *Galeus* reported from the eastern Pacific Ocean (Lavenberg and Fitch, 1966), represent a new species which is described here. The name proposed for the new species is from the Latin *piperatus* and refers to the peppered appearance of the ventral and lateral surfaces.

Galeus piperatus, new species

Figures 1 and 2

Holotype: Los Angeles County Museum of Natural History No. 7552, adult female, 302 mm. total length; R/V *Alaska* Station No. 64A2-16, at 28°55′N, 112°50.5′W, in the Gulf of California; 6 April 1964.

Paratypes: Los Angeles County Museum of Natural History No. 8818, immature female, 256 mm. total length; U.S. National Museum 200413, adult female, 296 mm. total length; both paratypes from R/V *Alaska* Station No. 64A2-16.

Comparative Material Examined: The holotype of *Galeus eastmani* (Jordan and Snyder) 1903, and four paratypes of *G. sauteri* (Jordan and Richardson) 1909, from the western Pacific; series of *G. arae* (Nichols) 1927, and *G. cadenati* Springer 1966, from the western Caribbean Sea; and *G. melastomus* (Rafinesque) 1810, and *G. polli* Cadenat 1959, from the eastern Atlantic. We have not seen specimens referable to *G. murinus* (Collett) 1904, *G. jenseni* (Saemundsson) 1922, from the northeastern Atlantic, or *G. hertwigi* (Englehardt) 1912, from Japan.

Diagnosis: Galeus piperatus, although not easily separated on the basis of one character alone, is distinct in that it has the following combination of

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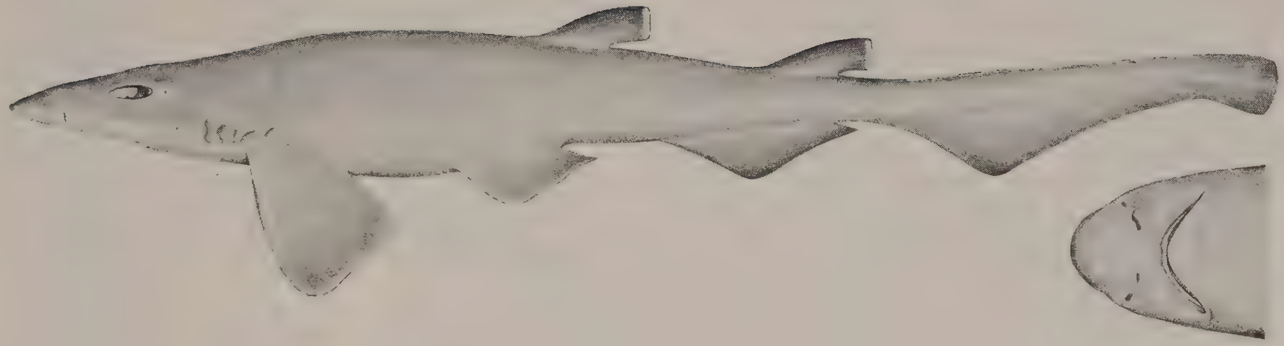

Figure 1. Galeus piperatus, new species, lateral view and ventral aspect of head of holotype, LACM 7552.

characters that distinguish it from all other species of scyliorhinid sharks: small size (females reach maturity at 30 cm.); a narrow crest of enlarged denticles on the dorsal edge of the caudal fin but no enlarged denticles on the leading edge of the lower caudal lobe, small denticles on the roof of the mouth anteriorly and on the tongue; a lack of well defined dorsal blotches in the adult, fine pepper-like spots on the ventral and lateral surfaces, each spot composed of a single melanophore; inside of mouth black.

Description of holotype: A 302-mm. female with characteristics of Scyliorhinidae: caudal axis not elevated; two dorsal fins and anal fin; dorsal fins nearly equal, origin of first just posterior to mid-point of base of pelvics; body long and slender, head long and somewhat depressed; caudal peduncle without precaudal pits; spiracles small, close to orbits; outer surface of nictitans entirely covered with denticles; conspicuous pores on lower side of snout.

Proportional measurements in percent of total length:

Trunk at pectoral origin: width, 9.9; height, 8.9.
Snout length in front of: outer nostrils, 3.3; mouth, 6.6.
Eye: horizontal diameter, 4.0; vertical diameter, 1.3.
Mouth: width, 8.3; length, 3.6.
Nostrils: distance between nasal apertures, 2.6.
Labial furrow lengths: upper, 1.3; lower 1.7.
Gill opening lengths: first, 2.6; fifth, 1.4.
First dorsal fin: vertical height, 3.0; length of base, 4.6.
Second dorsal fin: vertical height, 3.0; length of base, 5.3.
Caudal fin: upper margin, 28.5; lower anterior margin, 8.9.
Pectoral fin: anterior margin, 12.6; width, 8.9.
Pelvic fin: overall length, 11.6.
Distance from snout to: eye, 6.0; first gill-opening, 15.6; fifth gill opening, 21.5; first dorsal, 43.4; second dorsal, 61.9; upper caudal, 71.2; pectoral, 20.2; pelvic, 36.7.
Interspace between: first and second dorsal, 12.2; tip second dorsal and caudal, 2.3.

Dermal denticles small, numerous, covering entire body, three-pointed central one longest, typical shoulder denticles about 0.4 by 0.4 mm., denticles in crescent-shaped patch on anterior roof of mouth, 0.2 mm., leaf shaped (Fig. 2); greatest width caudal crest 1.25 mm., originating approximately 5.0 mm. from tip of second dorsal, largest scales in crest less than 1.0 mm. long.

Teeth small, numerous, similar in both jaws, about 31 rows on each side of upper jaw, 26 on one side of lower, largest tooth height about 1.0 mm.; upper teeth with five cusps, except tricuspid near center of jaw, middle cusp much the longest; lower teeth similar, central cusp lower toward angles of jaw; tooth arrangement alternate.

Total number of vertebrae 121; monospondylous vertebrae 33, caudal vertebrae 52.

General color grayish brown, dorsal surface somewhat darker, lighter ventrally, but demarcation between upper and lower surfaces not distinct; fins slightly darker than dorsal surface, but trailing edges of dorsals and pectorals marked by translucent bands about 1.0 to 2.0 mm. wide; entire body sprinkled with black melanophores 0.1 to 0.3 mm. diameter, especially noticeable on ventral surfaces; inside of mouth black.

Comparisons: Galeus piperatus, in comparison with all the specimens of *Galeus* that we were able to examine, is closest to *Galeus cadenati* from the Atlantic. *G. piperatus* differs from this species in having a shorter interdorsal distance, a shorter anal base, and longer gill slits. The color difference is marked as well. In the adult *G. cadenati*, dark brown saddles and blotches are present on the dorsal surface, and the dorsal fins are darker anteriorly and dorsally; the type of *G. piperatus* is devoid of dark brown blotches, and the paratypes have irregular and indistinct blotches that contrast little with the background color.

In *Galeus piperatus* a crest of enlarged denticles extends along the upper edge of the caudal fin from its base to about two-thirds the distance toward the tip. A caudal crest is present on all members of the genus *Galeus*, and, among other sharks of the family Scyliorhinidae, is also present on *Figaro boardmani*

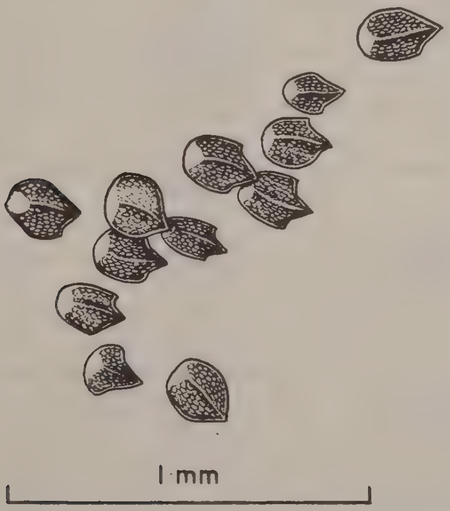

Figure 2. Camera lucida drawing of denticles that occur in a crescent-shaped patch located anteriorly on the roof of the mouth of *Galeus piperatus*, new species. Similar denticles are present on the tongue. We found mouth denticles in all species of *Galeus* that we examined. They differ from denticles of the external surfaces in being lanceolate instead of three-pointed and in being much smaller.

TABLE 1

Measurements, expressed as percent of total length, of the holotype and two paratypes of *Galeus piperatus* and two other species of *Galeus* from the Pacific. The table was prepared to conform with the tables given by Springer (1966) to facilitate comparison.

Species	*Galeus piperatus*	*Galeus eastmani*	*Galeus sauteri*
Number of specimens measured	3	1	4
Length range in millimeters	256-302	337	360-365
Tip of snout to—			
-anterior nasal aperture	3.3-4.3	3.0	3.1-3.9
-posterior nasal aperture	5.0-5.9	5.0	5.0-5.6
-front mouth	6.6-8.2	6.2	6.1-6.7
-eye	6.0-7.5	5.6	6.3-7.2
-gill I	15.6-17.1	14.8	15.6-16.7
-gill V	21.5-22.8	18.4	18.6-19.7
-origin pectoral	20.2-22.2	17.5	17.5-18.4
-1st dorsal fin	41.0-45.7	42.1	44.5-45.9
-pelvic fins	36.7-40.9	35.6	36.1-39.5
-anal fin	51.2-54.6	50.7	53.9-54.8
-2nd dorsal fin	45.4-61.9	62.3	63.3-63.9
-lower caudal fin	68.4-71.6	71.2	70.6-71.2
-upper caudal fin	68.6-73.0	71.2	72.0-75.1
-anus	40.7-44.7	38.0	40.6-43.6
Length upper caudal fin	28.3-29.7	29.7	26.7-29.5
Base 1st dorsal fin	4.6-5.1	4.7	4.2-5.3
Base 2nd dorsal fin	4.8-5.3	5.6	4.2-5.0
Base anal fin	12.6-13.3	11.9	11.7-13.9
Distance between dorsal fins	10.9-12.3	15.4	13.1-13.7
Internasal distance	2.6-3.1	2.1	2.2-3.0
Length orbit	3.9-4.4	4.2	3.6-4.2
Length lower labial fold	1.7-2.7	1.5	1.4-1.7
Length upper labial fold	1.3-2.0	1.2	1.4-1.9
Width mouth	8.3-9.2	6.2	6.0-7.0
Length mouth	3.6-4.8	3.7	3.8-4.7
Height gill I	2.3-2.6	1.5	1.1-1.4
Height gill V	1.2-1.4	0.9	0.8-0.8
Tip 2nd dorsal to caudal	1.0-2.3	1.5	1.9-3.1
Tip pelvic to 2nd dorsal	10.6-13.3	14.5	9.6-12.2
Tip pelvic to anal	2.0-2.6	5.0	2.2-3.3
Tip pelvic to lower caudal	18.4-19.9	24.3	16.7-19.7
Length outer margin pectoral	12.6-13.0	9.5	10.1-11.1
Length anterior margin 1st dorsal	7.8-8.9	7.4	6.7-7.5
Length anterior margin 2nd dorsal	6.8-7.8	7.4	5.5-6.7
Length anterior margin anal	5.9-7.6	5.9	5.3-6.4
Distance eye to spiracle	0.6-1.3	0.6	0.8-0.8

(Whitley) 1928, *Parmaturus xaniurus* (Gilbert) 1891, *Parmaturus pilosus* Garman 1906, as well as on *Apristurus profundorum* (Goode and Bean) 1896. *Figaro* is unique in having enlarged denticles not only on the upper caudal lobe but also on the leading edge of the lower caudal lobe. The denticle crest of *A. profundorum* lacks the much enlarged marginal denticles that are present in *Galeus*. The two species of *Parmaturus* have caudal crests similar to those in *Galeus*, but have shorter and thicker snouts and are generally much more robust.

As in other species of *Galeus*, the marginal denticles of the caudal crest of *Galeus piperatus* are larger than the central ones; the crest is structurally similar to crests in other members of the genus, but it is proportionally somewhat smaller. In comparison with specimens of equal size, the marginal crest denticles of *G. piperatus* are one-half as long as those in *G. arae*. The crest of *G. piperatus* differs from the crest of *G. sauteri* and *G. eastmani* in being narrower and having fewer denticles between the laterals.

The lining of the mouth is black or dusky in the type series of *Galeus piperatus*, whereas it is white or light colored in *Parmaturus xaniurus* and also in the preserved specimens of *G. sauteri* and *G. eastmani*. In some of the specimens of *G. melastomus* that have been in preservative for a long time the dark color of the inside of the mouth is entirely leached away; probably the color of the mouth lining would not always be reliable in distinguishing preserved specimens. It may be a useful field character in the eastern tropical Pacific for quick separation of *Galeus* and *Parmaturus*. Apparently the darker color of the mouth lining characterizes fresh specimens of all the Atlantic species of *Galeus* as well as *G. piperatus*. The mouth lining in *G. murinus* was described by Collett (1904) as blackish and in *G. jenseni* it was described by Saemundsson (1922) as dark violet.

The holotype of *Galeus piperatus* is grayish brown with the dorsal surfaces only slightly darker than the ventral surfaces and with almost no trace of markings. The paratypes, which are slightly smaller, show an indistinct and irregular arrangement of darker brown blotches dorsally, and the dorsal surfaces are appreciably darker. Very small and numerous black spots just large enough to be visible to the naked eye (0.1 mm.; 0.3 mm. when expanded) are scattered generally over the skin of all of our specimens; they are especially notable on the lower surfaces. Small, scattered spots of pigment are also found to some extent on *Galeus eastmani* and *G. sauteri*, but they are not so numerous or widely distributed. Pepper-like spots can be found on all members of the genus *Galeus*, but are more noticeable to the naked eye on *G. piperatus*. Unlike other species of *Galeus* that we have examined, *G. piperatus* has narrow, translucent bands 1.0-2.0 mm. wide without denticles on the trailing edges of the two dorsal fins; *G. cadenati* has wide colorless bands on the trailing edges of the dorsal fins, but these borders are covered with denticles and are not of uniform width.

Four measurements, expressed as percent of total length, indicate differ-

TABLE 2

Vertebral characters in seven species of *Galeus* from x-ray examination. Data for additional specimens of *G. arae* are given by Victor G. Springer and J. A. F. Garrick (1964).

Species of *Galeus*	Monospondylous vertebrae	Precaudal vertebrae	Caudal vertebrae	Total	A^1	B^2
piperatus type	33	69	52	121	153	116
piperatus	30	67	48	115	167	150
piperatus	31	67	51	118	157	129
eastmani type	33	82	57	139	165	122
sauteri paratype	33	75	49	124	139	128
sauteri paratype	33	74	47	121	150	138
sauteri paratype	34	76	47	123	138	118
sauteri paratype	32	77	47	124	148	121
cadenati	34	73	49	122	157	132
cadenati	33	73	46	119	147	122
arae	35	75	56	131	139	125
arae	36	76	54	130	169	123
arae	35	78	53	131	157	122
melastomus	37	80	61	141	150	115
polli	33	72	51	123	140	127
polli	34	71	54	125	145	145
polli	34	75	52	127	167	125
polli	34	74	51	125	170	121
polli	35	75	53	128	142	121

A^1 values $= \frac{\text{length penultimate monospondylous centrum}}{\text{length first diplospondylous centrum}} \times 100$ B^2 values $= \frac{\text{length penultimate monospondylous centrum}}{\text{diameter of penultimate monospondylous centrum}} \times 100$

ences in body proportions between *G. piperatus* and two other Pacific species: *G. eastmani* and *G. sauteri*. *G. piperatus*, with respect to these body proportions, appears to be transitional between the Atlantic and the western Pacific species, but tends to resemble more closely *Galeus cadenati* of the Atlantic.

The distance between dorsal fin bases, for example, is 10.9-12.3% of total length in *G. piperatus* and 15.4% in *G. eastmani* (it is 13.1-13.7% in *G. sauteri* and 12.3-14.7% in the Atlantic species, *G. cadenati*). The distance between the anal-fin tip and the caudal is much less in *G. piperatus* than in *G. eastmani* (1.7-2.7% as compared with 5.6%). This same distance in *G. sauteri* is 0.6-2.7%, putting *G. piperatus* close to *G. sauteri* with respect to this one measurement. The width of the mouth is 8.3-9.2% of the total length in *G. piperatus* as compared with 6.2% in *G. eastmani* and 6.0-7.0% in *G. sauteri*. (In *G. cadenati* it is 6.6-9.1% of total length). *G. piperatus* is not so slender as *G. eastmani* and *G. sauteri*, and is more like the Atlantic species (trunk height of the two adults of *G. pipcratus* measured at the pelvic fin is 9.2 and 10.9% of total length; similar measurement of *G. eastmani* is 7.4%, of *G. sauteri* 7.5-8.9%).

From the morphometric differences between *G. piperatus* and two other Pacific species, we can say that the new species has a shorter interdorsal distance, a wider mouth, and is shorter and heavier. A shorter anal-to-caudal fin distance also separates *G. piperatus* from *G. eastmani*.

Natural history notes: The holotype (302 mm.) and the larger paratype (296 mm.) each have a few large eggs about 7 mm. in diameter in the functional right ovary, and are considered sexually mature. The ovary of the smaller paratype (256 mm.), in gross examination, is much smaller and shows no indication of egg formation. This evidence suggests that *Galeus piperatus* reaches maturity at about 30 cm. or less. *G. piperatus* is thus one of the smaller species of the genus, only a little larger than *G. arae* and about the same length when mature as *G. cadenati*. Two species of *Galeus* (*G. melastomus* and *G. hertwigi*) are reported to reach lengths of more than 60 cm.

Whether *G. piperatus* lays eggs in egg cases or holds the embryos in the oviducts for development cannot be determined from the specimens examined. Within the genus *Galeus* it is known that *G. melastomus* lays eggs in leathery cases and *G. polli* bears living young (Cadenat, 1959).

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SUBSTITUTED NITROSALICYLANILIDES: A NEW CLASS OF SELECTIVELY TOXIC SEA LAMPREY LARVICIDES

Roland J. Starkey and John H. Howell

ABSTRACT

Structure activity relationships of substituted 3-nitro-and 5-nitrosalicylanilides and related compounds have been evaluated to elucidate their activity as potent selectively toxic sea lamprey larvicides.

Introduction

A substantial reduction of the sea lamprey in Lake Superior has been accomplished by the widespread treatment of larval habitat in streams with 3-trifluormethyl-4-nitrophenol (TFM) (Applegate, Howell, Moffett, Johnson and Smith, 1961). The larvicidal LD_{100} for this compound varies from 3-10 ppm depending upon the physical and chemical characteristics of the water in which it is used. The LD_{25} for 11 species of fish has been reported between 5 and 42 ppm (Applegate and King, 1962). During a continuing screening program to detect more potent, selectively toxic sea lamprey larvicides, substituted 3-nitro- and 5-nitrosalicylanilides were found to be more toxic to sea lamprey than TFM.

Salicylanilide was first used as a textile fungistat (Fargher, Galloway, and Probert, 1930), and later clinically in the topical treatment of dermatophytoses (Schwartz, Peck, Botvinick, and Leibovitz, 1946; Sullivan and Bereston, 1952). Derivatives of salicylanilide have exhibited a diverse bioactivity spectrum, including antimicrobial activity (Taborsky, Darker, and Kaye, 1959; Taborsky and Starkey, 1962; Taborsky and Starkey, 1963); antitumor activity (Taborsky and Starkey, 1962); molluscicidal function (Gönnert and Strufe, 1962); and as a taeniacide (Forbes, 1963). One of these compounds, 2′,5-dichloro-4′-nitrosalicylanilide (Bayer 73), has already been used successfully as a synergist of TFM in control of sea lampreys (Howell, King, Smith, and Hanson, 1964).

Preliminary mammalian oral toxicity studies with substituted 3-nitro- and 5-nitrosalicylanilides indicate lack of side effects in dosages greater than 2.5 gm/kg. Halo-3-nitrosalicylanilides, introduced by the intraperitoneal route in the rate, produce an LD_{50} of 35 mg/kg and halo-5-nitrosalicylanilides an LD_{50} of 125 mg/kg (Taborsky and Starkey, 1962).

Prompted by the results of preliminary larvicidal screening studies and the relatively low mammalian toxicity, it was decided to evaluate structure-activity relationships of a series of 3-nitro- and 5-nitrosalicylanilides and related benzanilides in an attempt to design more effective and selective sea lamprey larvicides. A similar study, undertaken during the development of halo-nitrophenols as sea lamprey larvicides (Applegate, Johnson, and Smith, 1966), is described in the preceding paper of this report.

This paper presents the general activity-relationships for selected compounds from this series. We believe this information, although preliminary, merits presentation on the following grounds: (a) agreement of structure-activity relationships with prior studies with salicylanilides (Baichwal, Baxter, Kandel, and Walker, 1960); (b) consistency of structure-activity relationships within our own data and, (c) correlation of preliminary screening data with compounds chosen for comprehensive evaluation.

Methods

Substituted 3-nitro- and 5-nitrosalicylanilides were prepared according to previously reported techniques (Taborsky *et al.*, 1959; Taborsky and Starkey, 1963). Included in the study were 3-nitrosalicylotoluidides, 3-nitro-salicyloxylidides, a 3-nitro-salicylanisidide, and miscellaneous benzanilides[1].

The facilities, methods, and various techniques used in evaluating sea lamprey larvicides were reported by Applegate *et al.* (1957; 1958). Minimal requirements for larvicidal selectivity have been documented (Howell and Marquette, 1962).

Results

Of one hundred salicylanilides and benzanilides, 80 demonstrated larvicidal activity at the maximum screening level of 10 ppm. Among these active compounds were 56 that exhibited selective toxicity for larval lamprey over fingerling rainbow trout, *Salmo gairdneri*, 13 which were equally toxic to both species and 11 more toxic to rainbow trout.

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[1] Method of preparation by Starkey unpublished.

Table 1 illustrates the obligatory molecular requirements for the *ortho* phenolic hydroxyl substituent in the carboxylic acid moiety of salicylanilide as depicted by the complete lack of activity in benzanilides. This finding conforms to the observations of Baichwal *et al.* (1960) in regard to the *ortho* hydroxy requirements for salicylanilide and derivatives for antifungal activity.

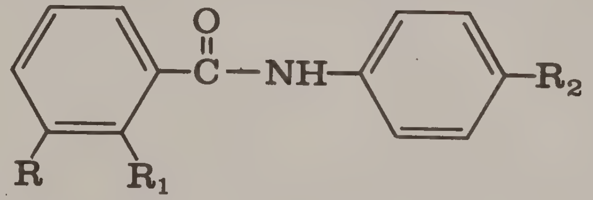
In addition, maximum toxicity and selectivity require the optimum combination of a halogen and a nitro group in the molecule. For example, salicylanilide and 3-nitrosalicylanilide, although active in concentrations less than 10 ppm, produce minimal selectivity. The addition of a halogen, as in 4′-chloro-3-nitrosalicylanilide, further increased toxicity and enhanced selectivity. Additional proof of the requirement for a nitro group in regard to selectivity is based on the reduction of this to an acetamido configuration (Taborsky and Starkey, 1963). The resulting 4′-chloro-3-acetamidosalicylanilide retains some of its toxicity but loses selectivity.

Mono-halonitrosalicylanilides, except 3 -chloro-5-nitrosalicylanilide, produced an LD_{100} for lamprey larvae at concentrations less than 10 ppm. Failure of this compound to exhibit an LD_{100} in concentrations not exceeding 15 ppm has been verified by repeated assays. Because this is the only 5-nitrosalicylanilide substituted in the *meta* position of the aniline moiety, studies are being undertaken with additional 5-nitrosalicylanilides substituted in the same position with other halogens to determine if the relatively low toxicity is position dependent.

Discussion

Larval toxicity of the mono-halonitrosalicylanilides generally falls into three levels at 0.3, 0.5, and 0.9 to 3.0 ppm, respectively. The importance of the halogen locus in relation to the toxicity of 3-nitro-and 5-nitrosalicylanilides is depicted in Table 2. *Meta* and *para* substituents in the aniline moiety of 3-nitrosalicylanilides produce a toxic effect at 0.3 ppm. In 5-nitrosalicylanilides substitution of a halogen in the *para* position results in a group of compounds consistently active at 0.5 ppm. Compounds larvicidal in the 0.9 to 3.0 ppm range are

Table 1. Comparison of molecular requirements for substituted mono-halo-nitrosalicylanilides exhibiting selective toxicity to larval sea lamprey and fingerling rainbow trout



Compound	Substituents			Lamprey	Trout
	R	R_1	R_2	LD_{100} (ppm)	LD_{25} (ppm)
Benzanilide	. .	. .	. .	>10.0	>10.0
4'-chlorobenzanilide	. .	. .	-Cl	>10.0	>10.0
Salicylanide	. .	-OH	. .	9.5	9.5[1]
3-nitrosalicylanilide	$-NO_2$	. .	. .	3.0	3.0
4'-chloro-3-nitrobenzanilide	$-NO_2$	. .	-Cl	>10.0	>10.0
4'-chloro-3-nitrosalicylanilide	$-NO_2$	-OH	-Cl	0.3	0.7
4'-chloro-3-acetamidosalicylanilide	-NH $COCH_3$	-OH	-Cl	3.0	3.0[2]

[1] LD_{75} at 9.5 ppm

[2] LD_{100}

Table 2. Comparative toxicity of halonitrosalicylanilides to larval sea lamprey and fingerling rainbow trout as a function of substituent loci.

Compound	Lamprey	Trout
	LD_{100} (ppm)	LD_{25} (ppm)
3'-chloro-3-nitrosalicylanilide	0.3	0.9
4'-chloro-3-nitrosalicylanilide	0.3	0.7
3'-iodo-3-nitrosalicylanilide	0.3	1.0
4'-iodo-3-nitrosalicylanilide	0.3	0.7
3'-bromo-3-nitrosalicylanilide	0.3	1.0
4'-bromo-3-nitrosalicylanilide	0.3	1.0
4'-chloro-5-nitrosalicylanilide	0.5	1.0
3'-fluoro-3-nitrosalicylanilide	0.5	0.9
4'-iodo-5-nitrosalicylanilide	0.5	1.0
4'-bromo-5-nitrosalicylanilide	0.5	1.0
2'-chloro-5-nitrosalicylanilide	0.9	3.0
2'-iodo-3-nitrosalicylanilide	1.0	3.0
2'-bromo-3-nitrosalicylanilide	1.0	1.0[1]
4'-fluoro-3-nitrosalicylanilide	1.0	3.0
2'-fluoro-3-nitrosalicylanilide	3.0	3.0
2'-chloro-3-nitrosalicylanilide	3.0	7.0
4'-fluoro-5-nitrosalicylanilide	3.0	-
3'-chloro-5-nitrosalicylanilide	15.0	15.0

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[1] LD_{100}

either *ortho* substituted 3-nitro- or 5-nitrosalicylanilides. Fluoro-3-nitro-and 5-nitrosalicylanilides deviated from this pattern and cannot be explained on the basis of our present data.

Toxicity to rainbow trout and the resulting selectivity is not as consistent as for larvicidal activity. Compounds that produce larval LD_{100} in the 0.3 to 0.5 range produced LD_{25}'s for trout in concentrations of 0.7 to 1.0 ppm. Again, the *ortho* substituted halo-3-nitro- or 5-nitrosalicylanilides and fluoro derivatives were less toxic to trout in the 3.0 to 15.0 ppm range. Although selectivity varied considerably among the compounds, those with the highest degree of larvicidal and trout toxicity were usually the most selective.

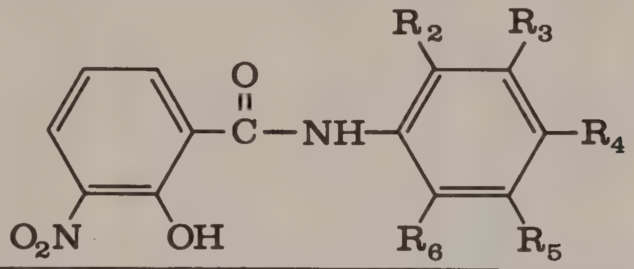
Comparative toxicity studies with substituted 3-nitrosalicylotoluidides, 3-nitrosalicyloxylidides, a 3-nitrosalicyanisidide, and a dichloro-3-nitrosalicylanilide are summarized in Table 3. These compounds have been arbitrarily subdivided into four groups based on substitutent patterns. The *ortho* hydroxy group in the acid moiety is common to all of the compounds while the *meta*, *para*, 5, and 6 position of the aniline moiety have been varied.

In all tests the 3-nitrosalicyloxylidides are less toxic to lamprey larvae than their corresponding substituted 3-nitrosalicylotoluidide. The only exception was with 3-nitrosalicyloxylidide but it was not tested at sufficiently high levels to determine if it is selective.

The loci of substituents in the aniline moiety of polysubstituted compounds appear to be correlated with toxicity to larval lamprey and rainbow trout. Also, dichloro substitutions evoke more potent activity than do chloro or methyl groups in the same positions. Activity becomes optimum when substitutions are made at the 2 and 5 positions in the aniline moiety as illustrated by 2′,5′-dichloro-3-nitrosalicylanilide. Activity was minimal with compounds substituted at the 2 and 6 positions.

Structure-activity relationships seem to exist among other 3-nitro-and 5-nitrosalicylanilides screened. The data are of such a preliminary nature that we have mentioned only the more obvious correlations. For example, 4′-chloro-3-nitrosalicylanilide is more toxic to larval lamprey than to trout, but an inverse toxicity exists with 4′-phenylazo-3-nitrosalicylanilide. Certain dinitrosalicylanilides are moderately toxic to larval lampreys and demonstrate some selectivity. Substitution of more than two halogens in the aniline moiety produces a saturation effect and a loss of toxicity and selectivity. Many additional benzanilides have been tested in addition to those listed in the tables and in no instance were they active at the 10.0 ppm screening level.

Table 3. Selective toxicity of polysubstituted 3-nitrosalicylanilides to larval sea lamprey and fingerling rainbow trout as a function of atomic loci



Compound -3-nitrosalicylanilide	Substituents					Lamprey	Trout
	R_2	R_3	R_4	R_5	R_6	LD_{100} (ppm)	LD_{25} (ppm)
2', 3'-dimethyl-	$-CH_3$	$-CH_3$	. .	. .	. .	3.0	5.0
2'-methyl-3'-chloro-	$-CH_3$	-Cl	. .	. .	. .	0.7	1.0
2', 4'-dimethyl-	$-CH_3$	. .	$-CH_3$	. .	. .	3.0	7.0
2'-methyl-4'-chloro-	$-CH_3$	. .	-Cl	. .	. .	0.5	0.7
2', 5'-dimethyl-	$-CH_3$	. .	. .	$-CH_3$	. .	1.0	3.0
2'-methyl-5'-chloro-	$-CH_3$	. .	. .	-Cl	. .	0.5	0.9
2', 5'-dichloro-	-Cl	. .	. .	-Cl	. .	0.3	0.9
2'-methoxy-5'-chloro-	$-CH_3O$	. .	. .	-Cl	. .	0.7	1.0
2', 6'-dimethyl-	$-CH_3$	. .	. .	. .	$-CH_3$	>10.0	>10.0
2'-chloro-6'-methyl-	-Cl	. .	. .	. .	$-CH_3$	0.7	1.0

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A TECHNIQUE FOR BLEEDING CHICKENS FROM THE JUGULAR VEIN

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The standard technique for obtaining large quantities of blood (50 c.c.) from chickens usually involves cardiac puncture (Sloan and Wilgus, 1930; Andrews, 1944; Genest, 1946; MacArthur, 1950). Law's (1960) method for obtaining blood samples from the jugular vein of turkeys, has had limited success when applied to chickens. A somewhat different technique, successfully used by the authors for a number of years, which facilitates quantity bleedings from the jugular vein of chickens is described here

METHOD

When bleeding chickens from the jugular vein, the operator should hold the head of the chicken in the palm of his left hand, with the bleeding apparatus aimed towards the body of the bird, while an assistant restrains the bird on its left side (Figure 1). Normally the right jugular vein is situated beneath the lateral neck space between the head and ventral feather tracts. The vein becomes prominent when occluded by the assistant applying pressure at the base of the neck. The operator uses his left forefinger to separate the trachea and vein and to act as a retaining fence against the vein. The needle is inclined towards the finger when puncturing the skin and vein wall. For quantity bleedings, a 50 ml. syringe is used with an 18 gauge needle.

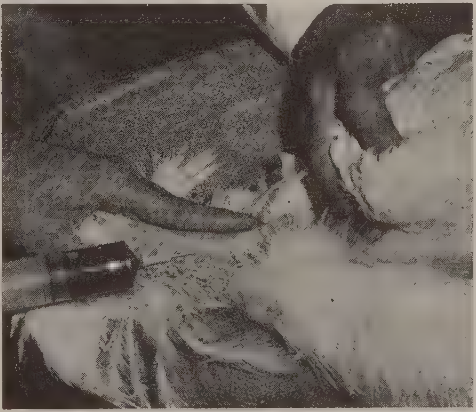

Fig. 1. Photograph showing technique for bleeding chickens from the jugular vein. The assistant's hand occludes the vein, and the operator's finger holds the vein immobile.

DISCUSSION

Unlike that of the turkey, the jugular vein of the chicken moves freely under the skin, offering no resistance to a needle. It is necessary, therefore, to immobilize the vein in chickens in order to puncture the vein wall. This is accomplished by placing the forefinger along the neck parallel to the vein. Since the operator is in front of the bird, the bleeding needle is directed towards the bird's body, an orientation exactly opposite to that of turkeys. Chickens with white skin and little neck fat are most easily bled, yellow skin and excess fat obstruct the view of the vein.

The advantages of the jugular vein over the heart and brachial veins as a source of blood samples have been listed by Law (1960). We also recommend the right jugular vein as a site of intravenous injections.

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January, 1966

Second International Oceanographic Congress, Moscow, May 30-June 8, 1966, p. 349-350

No. 408 — SIb

THE WATERS OVER THE SHELF OF THE NORTHERN GULF OF MEXICO AFTER HURRICANE BETSY: SEPTEMBER, 1965

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Hurricane Betsy entered the Gulf of Mexico on September 8, 1965, after crossing the southern tip of Florida. The storm followed a northwesterly path and penetrated the coast to the west of New Orleans, Louisiana, in the late hours of September 9. Hurricane-velocity winds extended 130 kilometers from the center and wind speeds of 190 km/hr were measured near the «eye». The average forward speed of the storm as it crossed the Gulf of Mexico was 24 km/hr.

The R/V «Alaminos», Texas A&M University, cruised along the edge of the continental shelf and occupied a series of bathythermograph stations on August 23-24, 1965. Immediately following the storm, on September 12-13, the «Alaminos» again cruised the same track. Ten days later, September 20-22, the M/V «Gus III», Bureau of Commercial Fisheries, occupied stations made earlier by the «Alaminos». From the data collected on these cruises, analyses can be made of the water structure before and immediately after the hurricane, and an insight gained of the rate at which waters affected by a violent storm may return to normal, seasonal conditions.

In August, the waters near the Mississippi Delta had a surface brackish layer spread over waters of normal salinity. The top of the thermocline was bounded by the 28° C and 29° C isotherms and began at depths of 20 to 30 meters. The thermocline was nearly horizontal, in an east-west direction, and the net water motion was parallel to the coast.

The temperature structure shortly after the passing of Hurricane Betsy was considerably different from that which prevailed in August. The thermocline was deeper in all waters than it was in August with the depth of the top varying from 40 to 90 meters. The greatest depths to the thermocline were in those waters which lay under the «eye» of the storm. The isotherm marking the top of the thermocline differed from the August condition, being lower by 2°-3° C along much of the section, and differed from one place to another along a transect across the path of the hurricane. Beneath and for about 130 kilometers to the east and west of the «eye» path, the top of the thermocline was bounded by the 26° C isotherm. Beyond 130 kilometers, the isotherm at the top of the thermocline was either 27° C or 28° C, but in all areas it was at least 1° C less than in August. Above the thermocline, there was little indication of brackish water.

Ten days after Hurricane Betsy had crossed the northern shelf of the Gulf of Mexico, the depth to the thermocline beneath and to the east of the path of the storm lay at depths of between 40 and 50 meters. To the west of the path the top of the thermocline was between 20 and 50 meters. In all waters except those immediately beneath the path of the storm, the top of the thermocline was bounded by the 27° C isotherm. Beneath the «eye» path, 26° C continued to mark the top. Brackish water had returned to the surface layers and was evident to the west of the mouth of the Mississippi River.

It is clear that the waters over the northern shelf of the Gulf were profoundly modified by the hurricane. The typical surface waters next to shore were removed and replaced by waters with oceanic characteristics. The influence of the hurricane extended to the greatst depths of the continental shelf (75 meters) so that water temperatures on the shelf floor were as much as 6° C warmer after the storm than before. Upwelling in the upper 30 meters of the water column was evident at distances of about 90 kilometers either side of the «eye» path of the hurricane. A 50-meter thick layer of isothermal water lay on the surface at distances of about 150 kilometers either side of the path. A strong divergence developed seaward of the Mississippi Delta. Surface currents flowed to the east and west on respective sides of the Delta. Although modified to some degree, these latter features were still present 10 days after the storm had passed over the northern shelf.

Proceedings of the Hawaiian Academy of Science
Forty-first Annual Meeting, 1965-1966, p. 18.

Abstract

1. BUREAU OF COMMERCIAL FISHERIES OPERATIONS WITH THE SUBMARINE ASHERAH AND ICHTHYOLOGICAL RESULTS OF THESE OPERATIONS

The Honolulu Laboratory of the Bureau of Commercial Fisheries operated the two-man submarine *Asherah* off Barber's Point, Oahu, during September and October, 1965. The craft was leased from General Dynamics/Electric Boat to gain experience with a submarine as a research tool. The research vessel *Townsend Cromwell* and the raft *Nenue II* provided support facilities for *Asherah*.

Asherah is 17 ft long, weighs 8,500 lbs, has an operational depth of 600 ft, and a speed of 2.5 knots. Research facilities include six portholes, two floodlights, an externally-mounted still camera and stroboscopic flash, a closed-circuit television camera and monitor, a depth gauge, and a fathometer. In addition, a hydrophone and plaques bearing materials of known reflectance were mounted on the hull.

The Bureau's research missions undertaken with *Asherah* included surveys of the midwater and bottom faunas, studies of the plankton community, patrols around submerged lights, evaluation of plankton nets and expendable bathythermographs, measurement of currents, observations at the thermocline, and measurements of light attenuation and biological sound. A total of 50 dives was made.

The survey area consisted of a gently shelving sandy plain extending from the shore to a depth of about 350 ft. At the 350-ft point the plain gave way to a precipitous limestone cliff, which dropped away to depths of several thousand feet. The submarine explored the plain from a depth of 80 ft to its brink and investigated the cliff face down to a depth of 630 ft.

The fish fauna of the plain was concentrated over ledges, isolated rocks, or patches of coral offering shelter. Only a few species, mostly triggerfish, were regularly encountered over the bare sand. This was in great contrast to the hordes of colorful species seen over rocks and coral. Prominent in these assemblages were butterflyfish, surgeonfish, damselfish, and goatfish. Many isolated rocky patches were cleaning stations for the wrasse *Labroides phtirophagus*. Swimming pelagically above the plain were large schools of mackerel scad, big-eye scad, and surgeonfish (*Naso hexacanthus*).

The steep cliff was rather featureless, and the more demersal fish were again concentrated in whatever ledges and crevices occurred. They included squirrelfish, eels, and butterflyfish. Enormous schools of 1-3 in. fish ranged along the cliff face; two captured specimens were juvenile *Holocentris lacteoguttatus*. Preying on these small fish were schools or small groups of skipjack, little tunny, wahoo, jacks, amberjack, and red and gray snappers. The cliff face served as a deep-water nursery ground as well as a rich forage area.

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Made in United States of America
Reprinted from Copeia, 1966, No. 3, September 7
pp. 475–477

Golem cooperae, A New Antennariid Fish from Fiji

Donald W. Strasburg

A new frogfish of the family Antennariidae is described as *Golem cooperae*. *Golem cooperae* differs from *G. cryptacanthus* (Weber), the only other species in the genus, in having the dorsal, caudal, and anal fins free instead of connected by membranes, and in having the skin covered with V-shaped dermal denticles. *G. cooperae* is based on a single specimen collected in two feet of water near Suva, Fiji.

RECENTLY, Mrs. Jane Cooper, my longtime friend and an amateur ichthyologist, sent to me from Suva, Fiji, a specimen of an antennariid fish which I have found to be an undescribed species referable to the genus *Golem*.

In his recent monograph of the Antennariidae, Schultz (1957:55, 81, 82) placed *Antennarius cryptacanthus* Weber in *Antennatus* (*Xenophrynichthys*), taxa erected to accommodate a phyletic line lacking an ilicium and with embedded dorsal spines. More recently, Schultz (1964:177) synonymized *Xenophrynichthys* with *Golem*, a name proposed earlier by Whitley (1957:70) for *cryptacanthus*. In his second paper Schultz accorded full generic status to *Golem*. In the present study it was found that the two species of *Golem* differ sufficiently from other frogfishes to merit generic recognition.

Golem cryptacanthus is characterized by smooth or slightly granular skin covered with low papillae; the dorsal, caudal, and anal fins connected by membranes; 12–14 simple dorsal rays; 7 simple anal rays; and 8 pectoral rays. *G. cooperae* has minute V-shaped denticles covering the skin giving it a shagreen-like texture, free vertical fins, 8 simple and 2 branched dorsal rays, 7 branched anal rays, and 10 simple pectoral rays. The two species of *Golem* can be separated by the following key:

1a. Dorsal, caudal, and anal fins connected by membranes; skin smooth or slightly granular .... *Golem cryptacanthus* (Weber).
1b. Dorsal, caudal, and anal fins free: skin covered with V-shaped dermal denticles .. *Golem cooperae*, new species.

I am grateful to H. Nijssen, Zoölogisch Museum, Amsterdam, and to G. P. Whitley, Australian Museum, Sydney, for examining type and other material of *G. cryptacanthus*.

Golem cooperae, n. sp.
(Figs. 1 and 2)

Holotype.—U. S. National Museum No. 199683, female, 140 mm standard length, 196 mm total length. Collected July 1964, by unidentified Fijian workmen who stoned

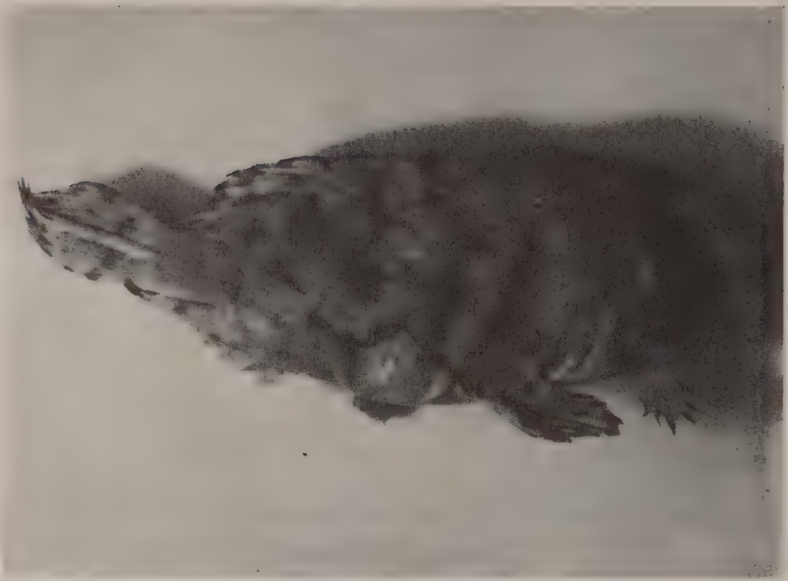

Fig. 1. *Golem cooperae* new species, holotype, lateral aspect.

it in 2 ft of water at the Cement Company Wharf, Bay of Islands, Lami, Viti Levu, Fiji. Lami is a mangrove-skirted area three miles northwest of Suva. This locality is not identified on U. S. Hydrographic Office Chart No. 2865, but borders Naingalongalo Harbor on the chart. The substratum at the type locality varies from soft mud to sand and rubble, with a considerable admixture of trash. The water is murky and teems with small fish.

Description.—Body stout and globular, the depressed profile shown in Fig. 1 probably caused by blows to the dorsum during capture; dorsal spines completely covered by skin, undetectable externally, not clearly seen in X-rays (Fig. 2); dorsal, caudal, and anal fins not interconnected; skin covered with minute V-shaped denticles; lateral line adorned with conspicuous arch-like papillae; sensory canals between eyes and across cheeks similarly adorned; dorsal rays 10, the last two branched and possibly arising from the same base; anal rays 7, all branched; pectoral rays 10, all simple; pelvic rays I, 5, the innermost ray split nearly to its base; caudal rays 4 + 5, all branched; vertebrae 19, the first apparently consisting of only a centrum and a neural arch; upper lip smooth, lower lip with about 10 fringed lappets on each side. Fig. 2 also shows that the vertebral column and some epaxial musculature were damaged when the fish was stoned.

Dentary with three rows of slender, depressible, nearly horizontal, posteriorly directed teeth; premaxillary teeth similar to those of dentary except that number of rows is about five at symphysis, three at midlength of premaxillary, and one near rictus; about five rows of slender depressible teeth on palatines and on expanded wings of vomer; a broad patch of similar teeth on each side of tongue, extending posteriorly to rear of mouth.

The damaged and somewhat flaccid state of the holotype precludes precise measurement. Nevertheless the following measurements were made (mm): standard length 140, total length 196, greatest depth 81, least depth of caudal peduncle 19.3, distance between verticals through caudal base and rear base of soft dorsal 13.5, head length (distance between verticals through snout tip and gill opening) 73, maxillary length 34.8, length of dorsal base 62, bony interorbital width 11.9, eye diameter 7.6, longest dorsal ray (fifth) 52, and longest caudal ray (fifth) 56.3.

Color in alcohol.—Ground color light brownish gray, darker on back; throat, breast, and

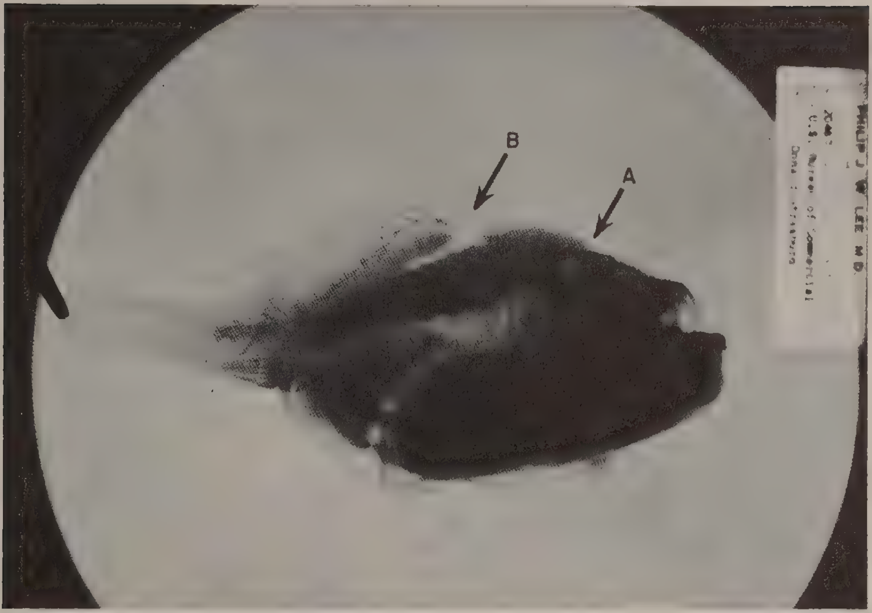

Fig. 2. Radiogram of *Golem cooperae* new species. Arrows indicate: (A) probable location of dorsal spines, and (B) region damaged by stoning during capture.

belly white; six or seven short black lines radiating from eye; body with black spots and lines arranged in curved rows which continue onto dorsal base; upper part of dorsal with round black spots; caudal with four rows of black spots; pectorals and anal with round black spots, the largest as big as eye; pelvic rays black posteriorly near tips; dorsal surface of pectoral base with two eye-sized black spots; another black spot, about half eye diameter in width, on each side of gill opening; floor of mouth gray.

Remarks.—In life, the color was bright yellow marked with black. The stomach contents of the holotype consisted of two well-digested fish originally about four inches long.

Specimens of *Golem* are rare in collections; the above is the fourth known specimen and the first from the central Pacific Ocean. The three other examples are referable to *G. cryptacanthus*; two were collected in the East Indies (Weber, 1913:564) and one from Papua (Whitley, 1957:70).

I am pleased to name *Golem cooperae* in honor of Mrs. Jane Cooper of Suva, Fiji.

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New Fish Records from Hawaii: *Hime, Pikea,* and *Omobranchus*

DONALD W. STRASBURG[1]

IN THEIR RECENT *Handbook of Hawaiian Fishes* Gosline and Brock (1960) record 584 species of fish from Hawaii, and point out that many more may be expected when depths greater than 100 ft are sampled extensively. About one new Hawaiian fish has been recorded each year since the Handbook's appearance, with most coming from deep water (Gosline, 1960: 28; Randall, 1961:58; 1963:432, 447; Strasburg, 1960:395). The present paper documents two new Hawaiian records obtained by deep handlining, and confirms the presence of a shallow-water blenny hitherto known only under peculiar circumstances.

Thanks are due Mr. Kuni Sakamoto of Honolulu for donating the handlined specimens, Mr. Joseph Harada of the Bureau of Commercial Fisheries Biological Laboratory in Honolulu for contributing the blenny, Dr. William A. Gosline for the loan of specimens in the University of Hawaii collections, and Mr. Tamotsu Nakata of the Bureau of Commercial Fisheries Biological Laboratory in Honolulu for preparing Figure 1.

FAMILY AULOPIDAE

Figure 1 depicts the first recorded Hawaiian specimen of the Aulopidae, an immature female of *Hime japonicus* (Günther). This fish was taken by bottomfishing with a handline at a depth of 780 ft. It was captured on April 15, 1963 by Mr. Kuni Sakamoto of the M/V "Koun Maru" of Honolulu. The capture site lies between Lanai and Kahoolawe, islands near the center of the main Hawaiian group.

Counts made on this specimen are: D 16, A 10, P 11–11, V 9–9, C 9 + 1 + 9, lateral line scales 43–43, transverse scale rows at level of fourth dorsal ray 3½ + 1 + 5½, predorsal scales 13, branchiostegal rays 13, and gill rakers on first arch 4 + 1 + 13. Measurements (in mm) are: standard length 219, head length 65, snout length 17.5, greatest eye diameter 17.7, greatest depth of body 41.3, least depth of caudal peduncle 16.2, snout to dorsal origin (diagonal) 77, length of dorsal base 64, snout to anal origin (diagonal) 165, length of anal base 23, longest dorsal ray (third) 41, longest pectoral ray (third from top) 39, longest pelvic ray (fourth) 44.5, longest anal ray (third) 20, greatest dimension of adipose fin 6.8, and width of bony interorbital 11.

The teeth are arranged in villiform bands in both jaws and on the vomer and palatines. The outer teeth are shorter than the inner ones. The center of the tongue bears an elongate band of tiny villiform teeth which are too small to be seen by the unaided eye, but which can be easily felt by probing with a finger or a needle. There is a single nostril on each side, guarded anteriorly by a small flap of skin.

The fish was frozen after capture and was thawed and photographed three days later. Its life coloration was as follows, based on a 35-mm transparency and field notes: Upper sides brownish-red, with dark-brown saddles running to the midsides beneath the anterior part of the dorsal fin, the posterior part of the dorsal fin, the adipose fin, and just before the caudal base. Interspaces between these saddles streaked with yellow pigment above lateral line. Lower sides silvery-white, blotched irregularly with vermilion. Throat, breast, and belly white; ventral side of tail and gill membranes lemon. Top of head olive-brown, cheeks silvery with red blotches, snout and opercle olive-brown with red blotches, iris yellow. Dorsal fin gray with round vermilion spots arranged in four irregular diagonal rows, largest spots about size of pupil; anal fin pale lemon; lower lobe of caudal yellow, with upper and lower rays streaked with red; upper lobe of caudal gray, blotched irregularly with lemon and red; pelvics lemon with orange blotches; pectorals hyaline with five vermilion

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[1] U. S. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii. Manuscript received August 12, 1964.

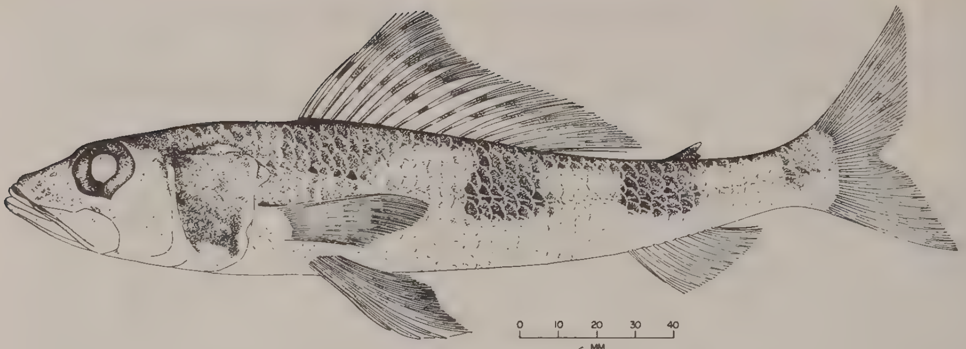

FIG. 1. Hawaiian *Hime japonicus* (Günther), 219 mm in standard length.

bands; adipose fin brown with red distal tip. This coloration agrees with that of the Japanese specimen figured by Kamohara (1955: pl. 9), except that his fish has only weak indications of spotting on the dorsal, caudal, and pectoral fins, and none at all on the cheeks and opercles.

In alcohol the Hawaiian *Hime* is dusky above and pale below. The four dark saddles persist, as does the gray ground color of the dorsal fin and upper caudal lobe. These fins are now white-spotted, for their vermilion pigment has faded completely.

The Hawaiian specimen agrees well with the description of the Japanese type given by Günther (1880:72) and with the brief account of other Japanese material presented by Matsubara (1955:240). *H. japonicus* can be distinguished from its only other congener, *H. damasi* (also from Japan), by its having 15 or 16 dorsal rays, about 43 lateral line scales, and an eye diameter about equal to the snout length, as compared with 14 dorsal rays, about 35 lateral line scales, and the eye diameter shorter than the snout in *damasi.* Among Hawaiian fishes *H. japonicus* superficially resembles the Synodontidae and the Chlorophthalmidae. It can be distinguished from the Synodontidae by its large eye, which is contained 3.6 times in the head length as opposed to 5–6 times in the Synodontidae, and from the Chlorophthalmidae by its long dorsal fin. The dorsal base is 3.5 times the eye diameter in *Hime,* and equals the eye diameter in *Chlorophthalmus.*

The specimen has been deposited in the U. S. National Museum (No. 198224).

FAMILY SERRANIDAE

A second unrecorded Hawaiian fish was taken with the *Hime* discussed above. This was a 214-mm male *Pikea maculata* Döderlein and Steindachner. Another unreported Hawaiian specimen of *P. maculata* was subsequently made available by Dr. Gosline. The latter fish, which is 213 mm in standard length, lacks collection data and its sex cannot be determined. Both specimens are essentially identical with Döderlein and Steindachner's illustration (Steindachner and Döderlein, 1883: pl. 6, fig. 1) of the Japanese type specimen, which is reproduced here as Figure 2.

Counts are the same for both specimens except for pectoral rays and scales. Both fish have D VIII, 12; A III, 8; VI, 5; C 17; branchiostegal rays 7; and gill rakers on the first arch 1 + 1 + 6 (there are also five flat patches of tiny denticles dorsad to the first raker and about four such patches ventrad to the last raker). The 214-mm fish has 68 pore-bearing scales in the lateral line, the 213-mm individual has 64. The 214-mm fish has 6½ + 1 + 31 scales transversely between the first dorsal spine and the anus, the 213-mm fish has 6½ + 1 + 32. The larger fish has a pectoral formula of i,14–i,14,i; the smaller has i,14,i in both pectorals. Schultz (1958:328) gives a pectoral formula of ii, 13 for Japanese *maculata,* but does not state the number of specimens examined or the range of variation in this character.

The teeth of *maculata* are needle-like and are closely set in bands on the dentary, premaxillary, vomer, and palatines. They are retrorse and depressible posteriorly. The tongue bears tiny asperities which cannot be felt with the finger but which crepitate when probed with a needle. The anterior nostril lies in a simple thin-walled tube about 2.5 mm in length; the posterior nostril is kidney-shaped and has a raised rim.

Measurements (in mm) made on the 214- and 213-mm specimens, respectively, are: head length 82, 83; snout length 24.2, 23.0; eye diameter 14.4, 15.3; snout to dorsal origin (diagonal) 96, 91; length of dorsal base 85, 85; snout to anal origin (diagonal) 157, 155; length of anal base 31.4, 29.3; longest D spine (third) 24.0, 21.8; longest D ray (seventh) 43.5, 43.0; longest A spine (third) 21.3, 21.7; longest A ray (fourth) 40.7, 39.8; longest pectoral ray (fifth from top) 58.6, 54.8; longest pelvic ray (second) 37.4, 40.3; width of bony interorbital 17.1, 15.0; greatest depth of body 64, 64; and least depth of caudal peduncle 35.9, 34.7.

The 214-mm fish was frozen after capture, and thawed and photographed three days later. Its colors were as follows, based on a 35-mm transparency. Ground color pink; upper sides and back covered with numerous scattered red, dark-red, and yellow spots about size of pupil, yellow spots tending to form lengthwise stripes across snout and opercle. Lower sides, belly, and breast plain pink. Anal and spinous dorsal pink, the tips of the rays yellow; soft dorsal pink with dark-red spots and narrow yellow edge; pectorals light red, the upper rays yellow; outer caudal rays yellow, inner rays pink, spotted with dark-red. Iris red with traces of yellow.

In alcohol this fish is pale straw-colored except for what were formerly the dark-red spots on its upper sides, head, and caudal fin. These persist as brown spots. The longest dorsal, anal, pelvic, and caudal rays are narrowly tipped with black.

The two Hawaiian *maculata* fit the description and figure of the Japanese type specimen described by Steindachner and Döderlein (1883: 234), and also agree with *maculata* as set forth in the keys of Okada and Matsubara (1938:197–198) and Matsubara (1955:621). There are slight differences in proportions between Hawaiian and Japanese specimens in that the Hawaiian form tends to be slightly slimmer, its lateral line is highest beneath the fourth and fifth dorsal spines (instead of the sixth or seventh), and the last dorsal spine is only slightly less than half the length of the longest dorsal ray (rather than "much shorter" than half this ray).

P. maculata can be distinguished from *aurora,* the other Hawaiian *Pikea,* by the following characters. *P. maculata* has anal rays III, 8; 64–70 pores in the lateral line; 8 gill rakers on the first arch; and is marked anteriorly and posteriorly with spots about the size of the pupil. *P. aurora* has anal rays III, 9; 48–51 pores in the lateral line, 21 rakers on the first gill arch, and numerous tiny spots, the largest about ⅓ pupil diameter in width, posteriorly on the body. Some of these data are from Schultz (1958:327) and from a specimen of *aurora* loaned by Dr. Gosline.

The 214-mm fish has been deposited in the U. S. National Museum (No. 198225).

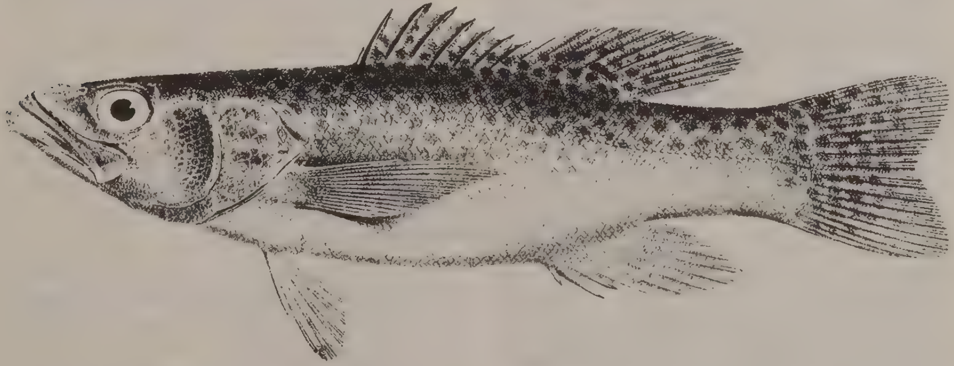

FIG. 2. Type of *Pikea maculata,* 25 cm total length. (After Steindachner and Döderlein.)

FAMILY BLENNIIDAE

Strasburg (1956:257) first recorded *Omobranchus elongatus* (Peters) from Hawaii on the basis of four specimens collected under peculiar circumstances. These fish were obtained from a concrete experimental tank located on Coconut Island, Kaneohe Bay, Oahu. The tank was supplied with running sea water, and at various times it housed experimental tunas, surgeonfish, exotic *Tridacna* clams, and other animals. The four *Omobranchus* were captured in the tank following draining; none have been taken since, in spite of years of intensive collecting in the Coconut Island area and elsewhere. It will probably never be determined how *Omobranchus* reached Hawaii, but the fact that one of the four original specimens was quite small suggested that it had been hatched in Hawaii, and that breeding populations therefore exist.

Mr. Joseph Harada, of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu, obtained a fifth Hawaiian specimen of *O. elongatus* on June 16, 1963. The fish emerged from a cavity in a lump of coralline rock when the rock was immersed in fresh water to clean it. The rock had been removed from a dead reef in Pearl Harbor, Oahu, at low tide two days earlier.

This newest Hawaiian *O. elongatus* agrees with the four specimens reported earlier. It is 56.3 mm in standard length, and is a male, judging from the ocellus in its soft dorsal. No gonad could be found. Counts made on it are D XII, 19; A II, 20; P 13–13; and number of pectoral rays encompassed by gill openings 6–6. It has a relatively short digestive tract for a blenny, and this was found to be packed with filamentous red, green, and blue-green algae along with large amounts of detrital matter and diatoms. Although *Omobranchus* has a prominent fang at the corner of each jaw, apparently it is a grazing herbivore. Perhaps the fangs aid in freeing algae from their attachments.

The capture of this specimen from an open reef in Pearl Harbor, on the opposite side of Oahu and 18 miles distant from Coconut Island, confirms the presence of native *O. elongatus* in Hawaii. Obviously its habitat has not been sampled very well. The specimen has been deposited in the U. S. National Museum (No. 198223).

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Observations on the Ecology of Four Apogonid Fishes

DONALD W. STRASBURG[1]

THE FISHES of the family Apogonidae are small, inconspicuous creatures which live in and around coral reefs. In the atolls of the central Pacific they are common, occasionally colorful, and sometimes occupants of specialized habitats. This paper reports aspects of the ecology of four species which are uncommon in collections: *Apogon novaeguineae* Valenciennes, which lives among the spines of the sea urchin *Echinothrix diadema* (Linnaeus); *Apogon leptacanthus* Bleeker, which occurs in vast shoals associated with the coral *Montipora gaimardi* Bernard; and *Apogon gracilis* (Bleeker) and *Gymnapogon gracilicauda* Lachner, which school in open water over reefs. Observations were made in the Marshall Islands during the summers of 1950, 1951, and 1955, when the writer participated in research projects sponsored by the Office of Naval Research, the University of Hawaii, and the Pacific Science Board of the National Research Council. Thanks are due these institutions as well as to the Military Air Transport Service and the Atomic Energy Commission who supplied transportation and many facilities. I also wish to thank Mme. I. Catala (Noumea Aquarium, New Caledonia), Dr. D. B. E. Magnus (Zoologisches Institut, Darmstadt, Germany), Dr. C. L. Smith (American Museum of Natural History, New York), Dr. R. A. Stevenson (University of Puerto Rico), and Mr. G. P. Whitley (Australian Museum, Sydney) for supplemental data.

Apogon novaeguineae Valenciennes

Visits were made to a number of atolls in the Marshall and Gilbert groups, but *A. novaeguineae* was found only at Eniwetok in the northern Marshalls. Here it occurred in the lagoon off Parry and Japtan Islands, and on the shallow ocean reef northwest of Cochiti Island. The fish was seen on 33 occasions, 23 times among the spines of the poisonous sea urchin *Echinothrix diadema*, and 10 times nowhere near an urchin. Both the fish and urchins lived in caves or beneath ledges, neither occurring in less than 4-ft depths and most living between about 8 and 18 ft. The number of fish per urchin ranged from 3 to 12, with 4 or 5 being usual.

Another apogonid, *Paramia quinquelineata* (Cuvier) sometimes accompanied *A. novaeguineae* among the urchin spines, while several other species were found in urchins lacking *novaeguineae*. These were *Apogon fraenatus* Valenciennes, *Apogon savayensis* Günther, *Apogon novemfasciatus* Cuvier, and the pipefish *Doryrhamphus m. melanopleura* (Bleeker). The occurrence of these four fishes among urchin spines was uncommon and usually involved only one or two individuals in a particular urchin. The attitude of these spine-dwelling species was horizontal except for *Doryrhamphus*, which oriented parallel to the nearest spines with its head toward the urchin's test.

Most of the above spine-dwelling fishes bear lengthwise stripes, the exception being *A. savayensis*. This is a drab species which neither matches nor contrasts with the urchin and probably occurs among its spines only occasionally. *A. novaeguineae*, on the other hand, is one of the most brightly colored apogonids, and its brilliant yellow contrasts vividly with the black or deep red of the urchin.[2] Its stripes are in-

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[2] A description of the color of living *novaeguineae* could not be found in the literature and therefore is presented here. Ground color of body light yellow, with gold and silver iridescence on sides of head and trunk. Throat and gill membranes white, rest of head yellow with scattered dusky pigment, giving it a dirty appearance. Five narrow white lines on head and body: first from occiput to first dorsal, where it bifurcates and runs along dorsal bases to caudal peduncle; second from interorbital along top of head and trunk parallel to first, uniting with its mate on dorsal edge of caudal peduncle; third from tip of snout across iris,

conspicuous and in no way tend to camouflage the fish.

A number of other fishes have been reported to inhabit sea urchin spines. Most of these bear contrasting stripes or bars which may match the spines in size and color. Such ecological situations have been found elsewhere in the Apogonidae (Abel, 1960*a*:482, 1960*b*:34; Lachner, 1955:43; and Magnus, in press), Gobiesocidae (Briggs, 1955:141; Mortensen, 1940:250; and Pfaff, 1942:413), Centriscidae (Davenport, 1955:37; Herald, 1961:151; and Le Danois et al., 1957:121), and the sciaenid *Eques*, the clinid *Malacoctenus aurolineatus*, the gobiids *Gobiosoma multifasciatum* and *G. novemlineatum*, and the gobiesocid *Acyrtus rubiginosus* (C. L. Smith, personal communication).

Some spine dwellers match the urchin's color but lack stripes. These include the apogonids *Siphamia zaribae* (Whitley, 1959:16), *S. versicolor* (Eibl-Eibesfeldt, 1961:57), several species of the gobiesocid genus *Arbaciosa* (Jordan and Evermann, 1898:2340-2343), some specimens of the gobiesocid *Acyrtus rubiginosus* (C. L. Smith, personal communication), and the Hawaiian pomacentrid *Dascyllus albisella* (R. A. Stevenson, personal communication). Of these, *S. versicolor*, at least, has a changeable color pattern which includes a striped phase. Peculiarly enough, its stripes appear only when the fish is away from its urchin host (Eibl-Eibesfeldt, 1961:58).

Some of the authors mentioned above state that spine dwellers should align their stripes with the spines if their color pattern is to provide an effective camouflage. Apparently this is done by *Paramia bipunctata, Aeoliscus, Doryrhamphus*, and possibly *Diademichthys*. These fishes are thus protected not only by the physical barrier of the spines, but also by the visual barrier of their camouflage. Such a dual safeguard may be necessary if their predators are capable of probing between the spines for food.

The other spine dwellers remain essentially horizontal, and their stripes are usually not aligned with spines. Obviously they are not camouflaged in this position, although the crisscross pattern of lines thus presented may disrupt the fish's outline. It is also possible that color and pattern are of little consequence once the fish is within the spine shelter. Certainly its brilliant yellow color is a blatant advertisement for *A. novaeguineae*.

A few observations were made on *A. novaeguineae* repopulation following departure of the fish from their urchin host. One urchin was removed from its cave and placed on open bottom 4 ft in front of the cave's mouth. A ridge on the bottom prevented the urchin from being seen from the cave. As soon as their host was disturbed, the *novaeguineae* left it and took shelter among the spines of a second urchin in the cave. The exposed urchin was watched for 15 minutes but no fish left the cave to join it. The urchin was then lifted over the ridge and placed 3 ft in front of the cave's mouth. In 2 minutes a single *novaeguineae* swam to the urchin and settled among its spines, followed by a second fish a few minutes later. The urchin crept to the cave's mouth during the succeeding 10 minutes, without being joined by additional fish. Two more *novaeguineae* joined it just as it crossed the cave's threshold. The balance of its original population of fish remained with the second urchin during an additional 5 minutes of observation.

On June 18, 1955, an isolated coral mound containing four large *Echinothrix*, each bearing several *A. novaeguineae*, was heavily treated with rotenone and all of the *novaeguineae* collected. This mound was visited regularly for several weeks, and then less frequently. No *novaeguineae* had returned by July 12, but there were a number of them among the spines of one urchin on August 24. This indicates that *novaeguineae* is rather restrictive in its movements. Unfortunately the distance to the next aggregation was not recorded.

Ten of the rotenoned specimens were examined for food consumed. Of these, two fish were empty and three others (males) had their stomachs packed with embryonated eggs. Probably these fish had been brooding eggs in their mouths and swallowed them under duress. Of

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touching upper edge of pupil, thence across midsides to caudal base; fourth from upper lip across iris, touching lower edge of pupil, thence across midsides to end of trunk; fifth from lower lip across suborbital to rear edge of opercle. Lines iridescent blue-white on head but faintly dusky on body. Tip of snout and lips sometimes red-orange. Iris yellow. Pectorals pale, other fins light red.

the five with food in their stomachs, four contained callianassid-like burrowing shrimp, two had ordinary shrimp, one a crab, one contained mysids, and one an unidentified crustacean. Additional food items have been reported by Hiatt and Strasburg (1960:80). None of these food organisms seemed to be an urchin commensal, and therefore it is probable that the fish left their spine shelters to feed. This is not necessary for all spine dwellers, as illustrated by Pfaff's observations (1942:416) of *Diademichthys* feeding on the tube feet of *Diadema* and on the sessile eggs of a shrimp living among the spines. Rivero (1950:115) mentions but does not name certain inquilinistic fishes which feed on colonial hydroids and other invertebrates living on sea urchins, and Eibl-Eibesfeldt (1961:57) describes *Siphamia versicolor* picking at and probably cleaning the test of *Diadema,* which had previously inclined its spines in a possible cleaning posture.

Apogon leptacanthus Bleeker

A. leptacanthus was found at only one locale, the lagoon side of Uliga Island, Majuro Atoll, Marshall Islands. This apogonid was always associated with the low branching coral *Montipora gaimardi* Bernard. Large growths of *M. gaimardi* were conspicuous at the swimming beach near the Uliga airstrip, and much smaller patches were seen near the Uliga causeway. The water depth over these reefs was 2–6 ft. The fish occurred in sheetlike schools, one or two fish deep, which drifted about 1 ft above the *Montipora* branches. On the approach of a swimmer the school gently subsided into the coral, to emerge after his departure.

The most impressive features of the *A. leptacanthus* schools were the large numbers of individuals and the fact that the environment was quite different from the open-water situation in which schooling usually occurs. The largest school seen was found over a rectangular patch of *Montipora* measuring 60 by 80 ft. About half of this rectangle was occupied by the school, which contained 10–25 fish per sq ft according to numerous estimates. These figures give a school abundance estimate of 24,000–60,000 fish, certainly a remarkable concentration for any reef species. The number of fish in two other schools was estimated in the same way; one contained 2,000–5,000 fish, and the other 500–1,250 fish.

Part of one of the *Montipora* beds was treated with rotenone to determine which other fishes coexisted with such dense concentrations of a single species. The only other fish which could be termed common was *Apogon snyderi* Jordan and Evermann. The following were taken in small numbers: *Chaetodon auriga* Forskål, *C. trifasciatus* Mungo Park, *C. lineolatus* Cuvier, *Thalassoma quinquevittata* (Lay and Bennett), *T. hardwickei* (Bennett), *Holocentrus laevis* Günther, *Parupeneus trifasciatus* (Lacépède), *Plesiops melas* Bleeker, *Ctenochaetus striatus* (Quoy and Gaimard), *Dascyllus aruanus* (Linnaeus), *Abudefduf glaucus* (Cuvier), *Amphiprion melanopus* Bleeker, and *Corythoichthys* and *Gymnothorax* juveniles too small to identify. Such a fauna is typical of most Marshallese coral communities except that here all individuals were small, most being the young of moderate-sized reef fishes. The dense forest of coral branches probably served as a protected nursery area for these small fishes.

The *Montipora* beds were visited on several occasions in 1950, 1951, and 1955. The *A. leptacanthus* schools were always present and, in fact, were regarded as permanent features by Uliga residents. Obviously the nutritional needs of this large population were great. The stomach contents of four rotenoned *leptacanthus* were examined, and revealed their principal food to be crustacean plankters, mostly crab zoea. Presumably these were obtained while the fish drifted above the coral. No *leptacanthus* were seen to feed, but all were noted to head in the same direction, and were probably exhibiting rheotaxic rather than schooling behavior. Currents very probably convey planktonic food to the relatively stationary fish.

A brief color description of *A. leptacanthus* follows: ground color translucent olive-tan, traces of dusky pigment on snout. Iris, suborbital and supraorbital regions iridescent sapphire. Two short diagonal orange bars behind eye, two short vertical orange bars on opercle, and two more on sides above pectorals. A narrow yellow-white line on dorsal midline behind soft dorsal. Pelvics and pectorals reddish, anal with a basal red band and reddish rays. Soft dorsal and caudal rays are faintly reddish.

Apogon gracilis (Bleeker) and *Gymnapogon gracilicauda* Lachner

Unlike most Apogonidae, which dwell in close proximity to a sheltering substratum, *A. gracilis* and *G. gracilicauda* are apparently pelagic species. They were observed many times in the lagoon at Parry Island, Eniwetok Atoll, swimming in large, loose schools. Most schools were in the general vicinity of coral mounds at depths of 12–25 ft, but a few occurred over relatively featureless sand or coral rubble at the same depth. The *gracilis* schools were composed of several hundred individuals, whereas the *gracilicauda* schools were much smaller, consisting of perhaps 5–25 fish. The number of schools and the number of fish per school increased with the distance from shore.

Both fish were difficult to recognize as apogonids in life. Their pelagic occurrence was unexpected and their colorless glassy transparency made them hard to detect and characterize. The two could be told apart by the presence in *A. gracilis* of an internal black spot on the lower caudal peduncle and the black tip of its upper caudal lobe.

Morphologically, *Gymnapogon* is quite distinct from the rest of the Apogonidae and it is not surprising to find it occupying a different habitat. A summary of its physical peculiarities and their systematic significance has been presented by Lachner (1953:490). *Apogon gracilis,* on the other hand, is a typical apogonid and shows no particular adaptations to a pelagic mode of life (except possibly for its colorless transparency). The diet of four rotenoned *A. gracilis* consisted of pelagic crustaceans, mostly amphipods.

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Observations of vertical migrations of Chaetognatha in the Gulf of Guinea

by Paul N. SUND (1) and Kenneth C. CUMMINGS (2).

Introduction.

Investigation of the temporal and spatial distribution of particular species of zooplankton in the tropical Atlantic is a major aspect of the Zooplankton Ecology Program of the Bureau of Commercial Fisheries, Biological Laboratory, Washington, D. C. As one part of this investigation, a study of vertical migration was carried out during the International Co-operative Investigations of the Tropical Atlantic, Equalant III, aboard the R/V *Geronimo.* This report presents data on the Chaetognatha collected during the study.

Materials and methods.

The plankton samples on which this study is based were collected during a 19-hour period on 20 and 21 March 1964 with enlarged Clarke-Bumpus samplers (Paquette, *et. al*, 1961) at a single station in the Gulf of Guinea (00°00′ latitude, 004°00′W longitude). A bathythermogram, obtained before sampling began (fig. 1*a*), was used as a guide for selecting six sampling depths distributed above, within, and below the thermocline (fig. 4). Because the vertical distribution of temperature scarcely changed during the sampling (fig. 1*a-f*), it was not necessary to alter the depths origi-

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(1) Chief, Pelagic Predators Program, Bureau of Commercial Fisheries, Tropical Atlantic Biological Laboratory, Miami, Florida.

(2) Much of the work of this study was done as a summer student project by the junior author, a student at George Washington University, Washington, D. C.

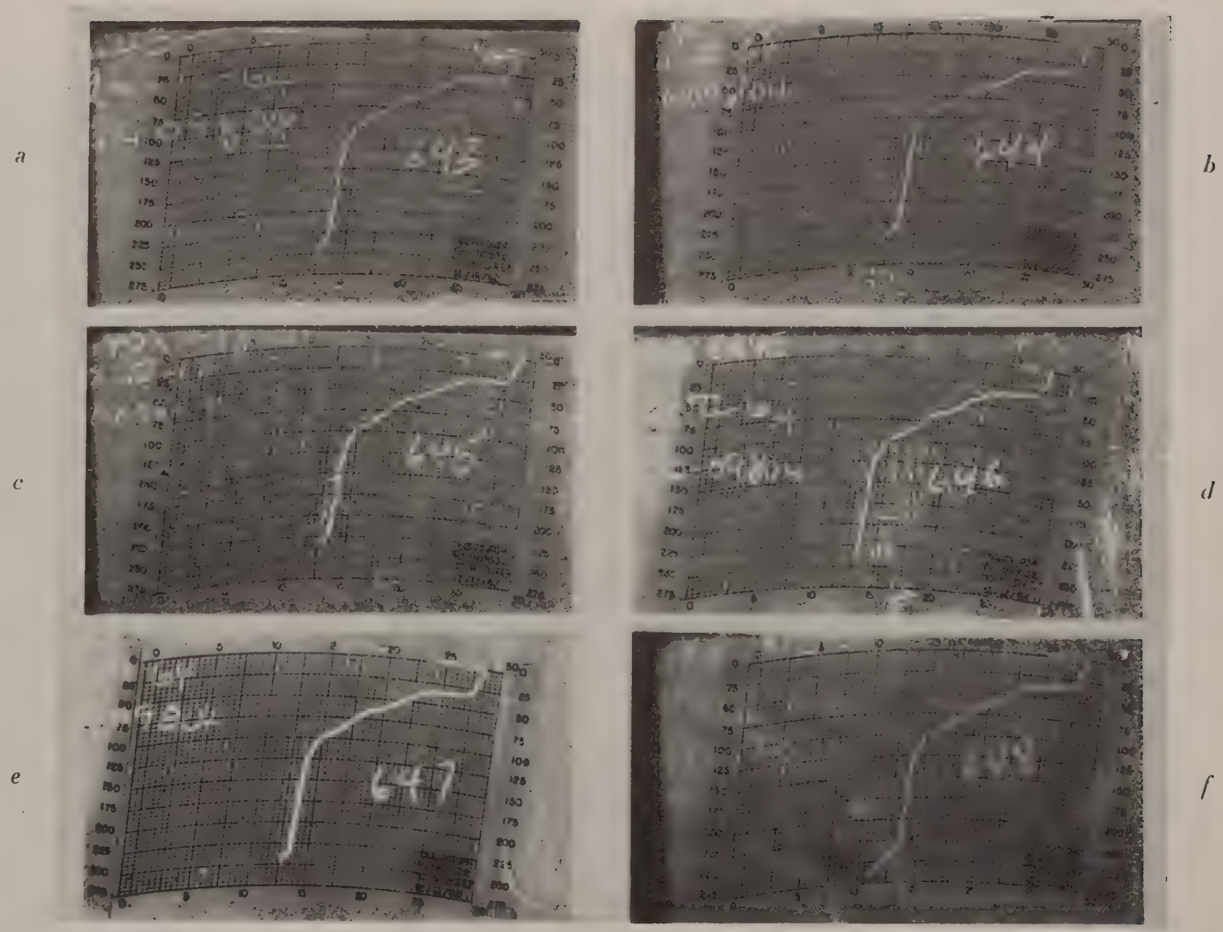


FIG. 1. — Bathythermograms taken prior to Clarke-Bumpus tows at GERONIMO station 188. The depth scale is in meters; temperature in degrees Celsius. The times of the observations (GCT) and the surface temperatures recorded were: (*a*) 1150, 29.8°; (*b*) 1550, 29.4°; (*c*) 1820, 29.3°; (*d*) 2245, 28.9°; (*e*) 0000, 28.5°; (*f*) 0245, 28.9°.

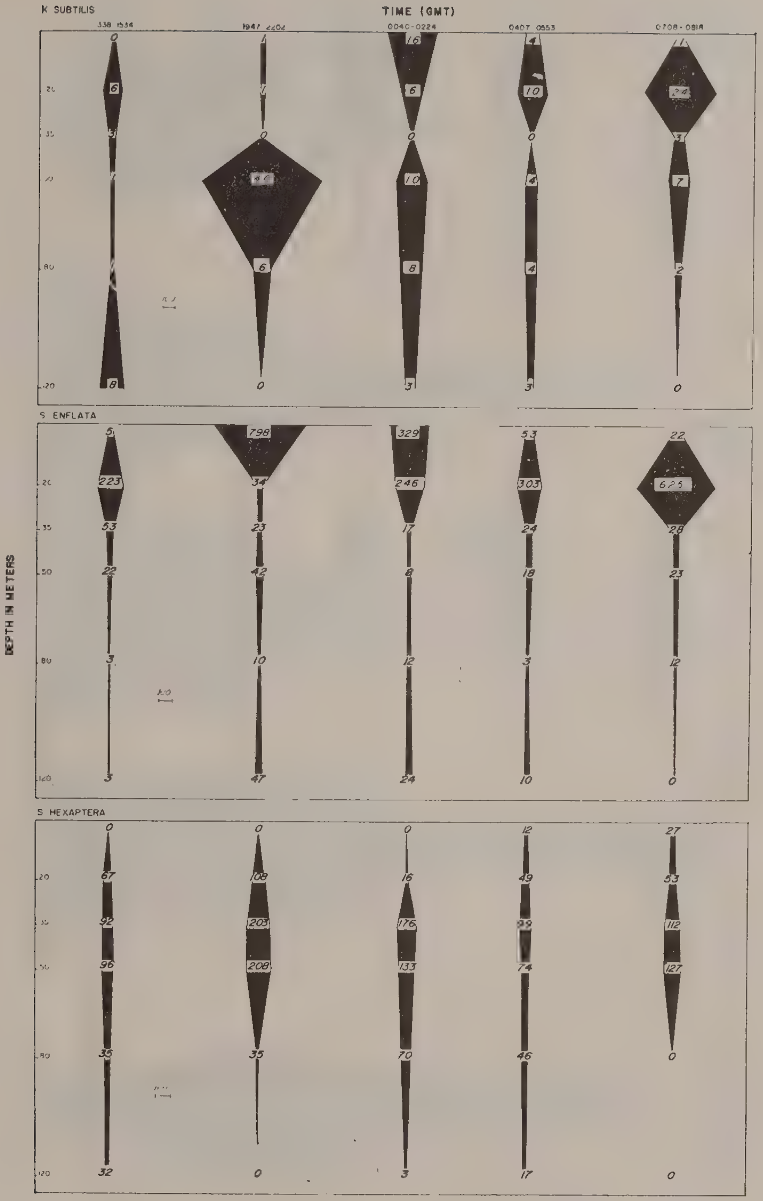
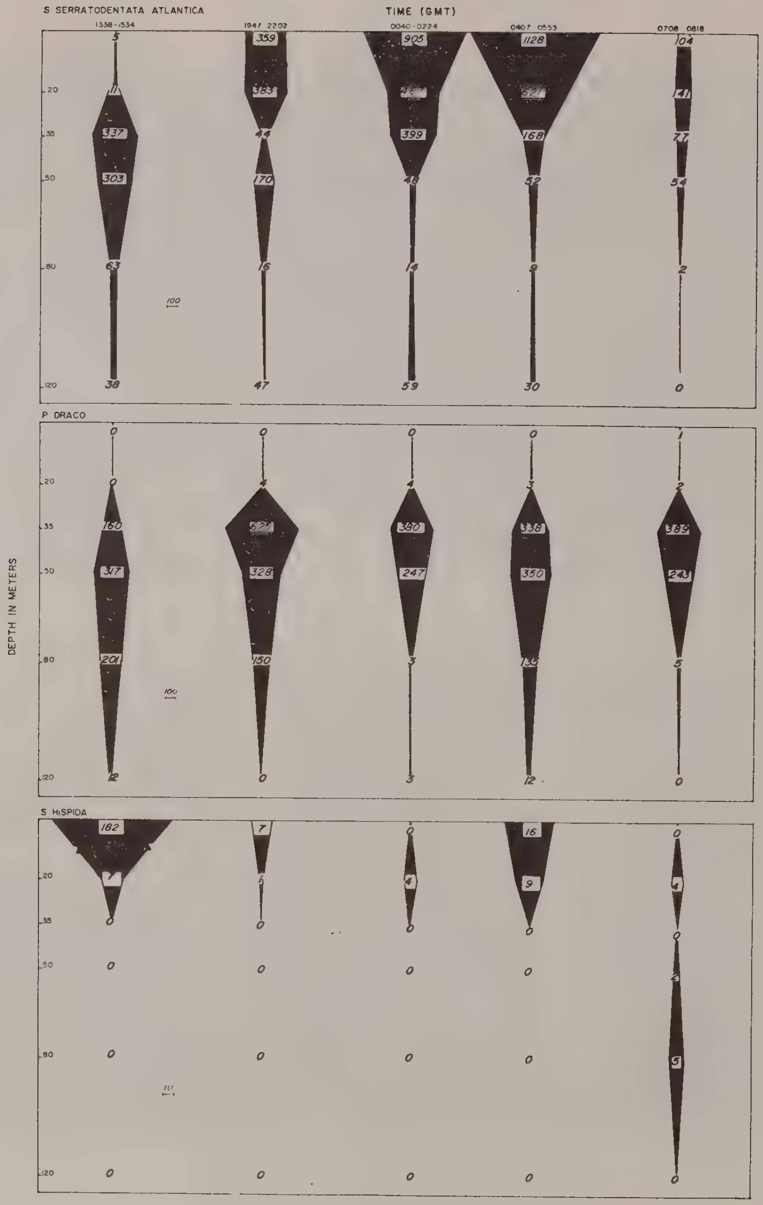


Fig. 2 *a*.

Vertical distribution of six species of chaetognaths at different times, 20-21 March 1964, Geronimo station 188, cruise 3 (00°00' latitude, 004°00 W longitude). The numbers of individuals are standardized to 1 000 m^3 of water strained. The scale of abundance is shown by the horizontal line in the lower left portion of each figure, Note the change of scale for the surface collection of *S. hispida*, at 1338-1534.


S SERRATODENTATA ATLANTICA
TIME (GMT)
1338-1534
1947 2202
0040-0224
0407 0553
0708 0818
5
359
905
1128
104
11
383
521
141
337
44
399
168
77
303
170
48
52
54
63
16
14
9
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0
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P DRACO
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0
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4
4
3
2
160
380
338
389
317
328
247
350
243
201
150
3
135
5
12
0
3
12
0
100
S HISPIDA
182
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DEPTH IN METERS
20
35
50
80
120

FIG. 2 *b*.

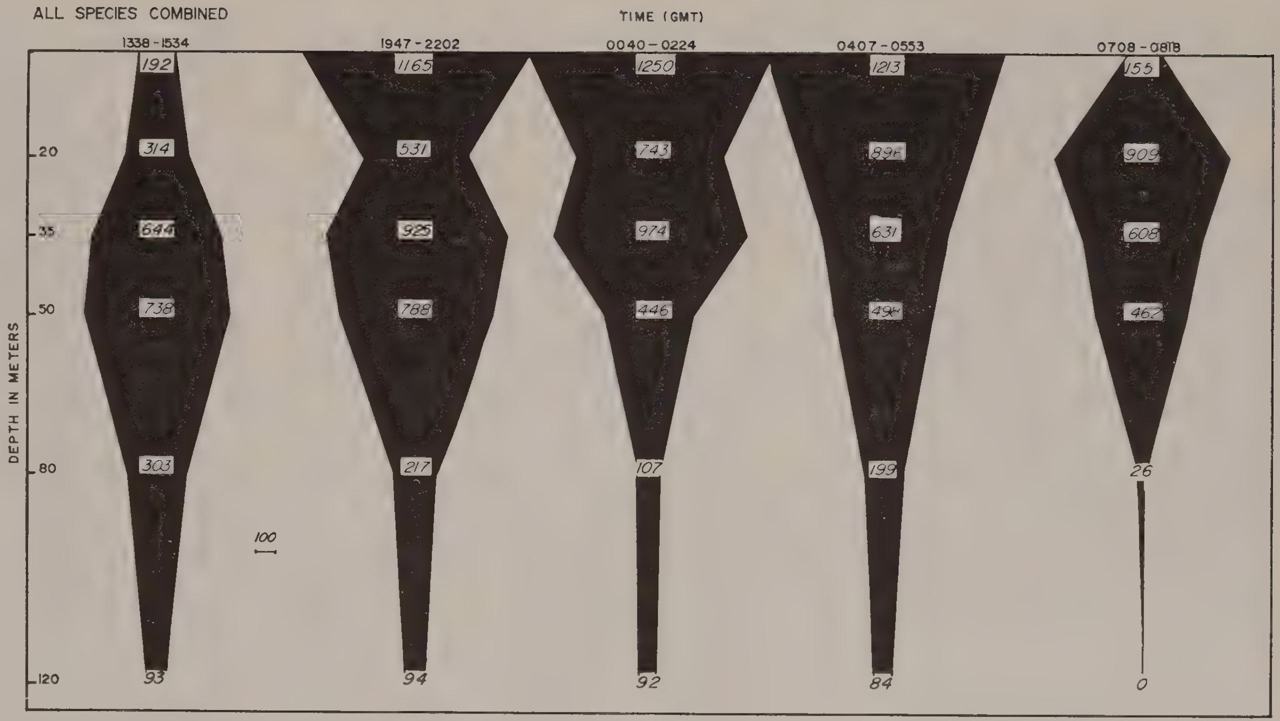

FIG. 3. — Vertical distribution of chaetognaths, all species combined, Geronimo station 188. The numbers of individuals are standardized to 1 000 m^3 of water strained. The scale of abundance is shown by the horizontal line (representing 100 individuals) in the lower left portion of the figure.

nally selected. Actual towing depths were calculated from the wire angle, assuming a straight wire. The tows were of 15-minute duration.

The chaetognaths were removed from the samples, identified to species and counted. These counts were standardized to number per 1 000 m³ of water filtered. A separate graph was drawn of the data for each of the six most abundant species to show vertical movements as a function of time (fig. 2). To determine if there was vertical migration by the chaetognath population as a whole, the total numbers of chaetognaths ib each sample, all species combined, were also graphed (fig. 3).

VERTICAL DISTRIBUTION AND MOVEMENT.

Nine species in three genera were identified : *Krohnitta pacifica* AIDA 1897 ; *K. subtilis* GRASSI 1881 ; *Pterosagitta draco* KROHN 1853 ; *Sagitta decipiens* FOWLER 1905 ; *S. enflata* GRASSI 1881 ; *S. hexaptera* D'ORBIGNY 1843 ; *S. hispida* CONANT 1895 ; *S. minima* GRASSI 1881 ; and *S. serratodentata atlantica* TOKIOKA 1940.

DUCRET (1962), SAINT-BON (1963), and LONGHURST (1964) have recorded not only the above species in the Gulf of Guinea but also *S. friderici* RITTER-ZAHONY 1911, *S. bipunctata* QUOY and GAIMARD 1827, *S. pseudoserratodentata* TOKIOKA 1940, *S. neodecipiens* TOKIOKA 1959, *S. lyra* KROHN 1853, *S. plactonis* STEINHAUS 1896, *Eukrohnia hamata* MOBIUS 1895. Apparently, however, no one has published information on the diurnal migrations of chaetognaths in these waters. The present study indicates diurnal vertical movement by *K. subtilis*, *S. enflata*, *S. hexaptera*, and *S. serratodentata atlantica*, but not by *P. draco* and *S. hispida* ; too few data were obtained to allow comment on K. *pacifica*, *S. decipiens*, and *S. minima*.

Data on the environment in which these organisms were found are summarized in figure 4. The values were determined from a Nansen-bottle cast made at the station 3 hours before the plankton sampling was started. The surface mixed layer reached a depth of approximately 35 m, and the bottom of the thermocline was between 100 and 125 m throughout the period of sampling.

The plot of total numbers of chaetognaths, all species combined, indicates movement toward the surface at night and a reversal of this movement after daybreak (fig. 3). Not all of the species were included in this diurnal vertical migration, however.

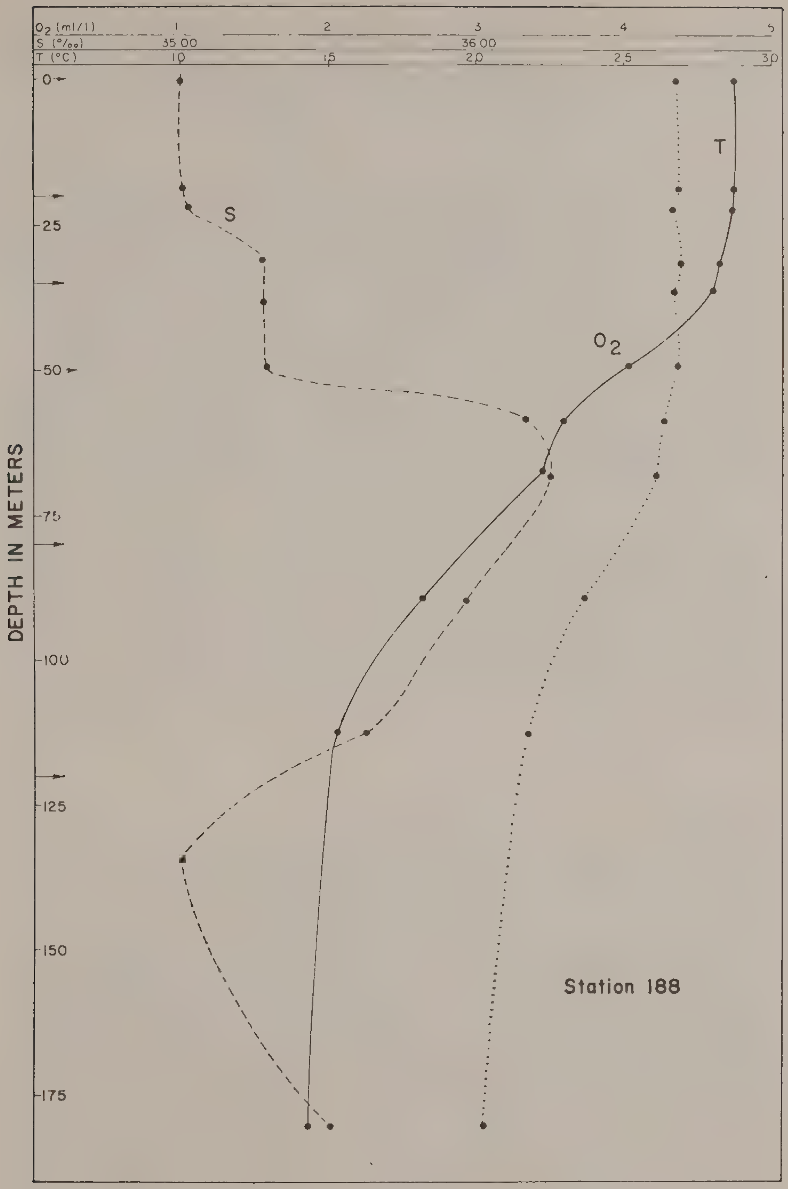

FIG. 4. — Vertical distribution of temperature (T°C), salinity (S °/oo), and oxygen (0_2, ml/1) at Geronimo station 188. The arrows at the left margin show the depths of sampling with Clarke-Bumpus nets.

ABUNDANCE AND DIURNAL MOVEMENTS OF INDIVIDUAL SPECIES (fig. 2).

Krohnitta subtilis. Few individuals were in the samples. An evening migration toward the surface from depths greater than 120 m (*Alvarino* 1964 ; *Sund* 1964) was indicated ; the greatest number were at the surface sometime between 2202 and 0040. The last two sets of samples indicated a return to depth that began before dawn.

The depth of the top of the thermocline (approximately 35 m) consistently coincided with low numbers of K. *subtilis.* The significance of this relation is not clear because the species apparently migrates through the thermocline. If the thermocline were a barrier to movement, one would expect to find *K. subtilis* either above or below it, but not, as was the case, both above and below.

Sagitta enflata. The greater numbers were consistently above the thermocline. Migration toward the surface between the first and second sampling periods was indicated. The numbers at the three shallowest sampling depths were most uniform in the midnight and early morning samples. Numbers were reduced at the surface after daylight. The vertical migration seemed to be confined to the upper 35 m of water, even though *S. enflata* was present at all depths sampled.

Sagitta hexaptera. The species was absent or scarce at the surface at all times of sampling. The greatest numbers occurred in the thermocline between 20 and 80 m, and especially at the 35 and 50 m sampling depths. Although evidence of vertical migration is not definite, the samples at 35 and 50 m tended to contain more *S. hexaptera* in the night than in the daytime. These higher numbers may be interpreted as the result of (1) sampling error, (2) nocturnal migration into that stratum from depths below 120 m, or (3) horizontal variations of the abundance of the species. The scarcity of the species in all the samples precludes making any real choice among these alternatives.

Sagitta serratodentata atlantica. This species exhibited a « classical » type of diurnal vertical migration. The afternoon samples showed a vertical distribution from the surface to 120 m and deeper, with by far the greatest concentration in the upper thermocline (35 and 50 m). After dark, the concentrations were greatest above the thermocline (at the surface and at 20 m). A progressive upward movement was indicated ; the maximum was at the surface in the predawn sample.

The final sample series, taken early in the morning, suggested a rapid departure from the surface after the predawn sample. The obvious general decrease in numbers in the final sample series is unexplained.

Pterosagitta draco. This species occurred only once at the surface. Below 20 m, the vertical distribution was nearly constant, with the greatest concentrations at 35 and 50 m. It seems that the surface layer may present environmental conditions unsatisfactory to this species.

Sagitta hispida. This species appeared only above the thermocline (surface and 20 m) except in the morning samples, when small numbers were collected at 50- and 80-m. No diurnal vertical migration was evident. The relatively large number at the surface in the first sample series is puzzling, but may have been due to swarming.

Krohnitta pacifica, *Sagitta decipiens*, and *Sagitta minima.* The numbers collected were too small to provide reliable evidence on vertical migration. The limited data agree with the vertical distributions of these species as reported from other geographic areas (SUND 1964, ALVARINO 1964), namely, that *K. pacifica* and *S. minima* usually occur in the epiplankton, whereas *S. decipiens* is mesoplanktonic.

SUMMARY.

Samples were taken with enlarged Clarke-Bumpus samplers at six depths on five occasions during a 19-hour period at a station in the Gulf of Guinea to obtain data on vertical migrations of zooplankton. This report considers only the Chaetognatha from these samples.

The combined numbers of the nine species captured indicate that appreciable upward movement took place at night and downward movement in the morning. The numbers of the individual species, however, demonstrate diurnal vertical movement by *Krohnitta subtilis*, *Sagitta enflata*, *S. hexaptera*, and *S. serratodentata atlantica* ; but not by *S. hispida* and *Pterosagitta draco*. The numbers of *K. pacifica*, *S. decipiens*, and *S. minima* collected were too small to provide reliable evidence on vertically migraton.

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Dolphin Impaled on Marlin's Bill

By PAUL N. SUND AND HENDRIK GIRIGORIE

FEEDING BILLFISHES are known to sometimes use their bills to stun their prey. Some authorities believe they may also occasionally stab other fishes just as they sometimes drive their bills into boats, ships, and mooring rigs (See "The Fisherman Fished," *Sea Frontiers,* 2-1, March 1956); but few personal observations of billfishes with prey impaled on their spears have been recorded. Recently, however, scientists from the Tropical Atlantic Biological Laboratory in Miami made such an observation in the Caribbean Sea.

On August 30, 1965, while steaming between Blanquilla and Grenada aboard the U.S. Department of the Interior's Research Vessel *Geronimo,* a marlin was observed swimming at the surface about 300 yards ahead of the ship. When approached to within about 100 feet it was seen that a female dolphin, *Coryphaena hippurus,* about 3 feet long was impaled on the marlin's spear. The marlin splashed the dolphin against the sea surface in an apparent effort to dislodge it. No further observations were possible, because the marlin sounded.

It is believed that this is only the second observation of a spearfish with prey impaled on its bill. In a paper in *Pacific Science* (12-1, 1958), Mr. R. L. Wisner of Scripps Institution of Oceanography discussed extensively the use of the bill in the feeding behavior of spearfishes and concluded, in part, that stabbings of prey probably are unintentional, or even accidental. Occasionally, persons have noted lesions on yellowfin and skipjack tunas and dolphins that appeared to be bill-scars. Dr. E. S. Iversen of the Institute of Marine Science, University of Miami, discussed these scars in an article in *Sea Frontiers* (5-3, August, 1959) and concluded that available evidence eliminated the possibility that such scars were caused by spearfishes.

Weighing 7,000 pounds in air and 3,800 pounds in sea water, Mobot is 5 feet around and 14 feet tall. The mechanical roughneck even swims in the water with two adjustable propellers, one on each side.

Far above, on a drilling ship, a man stationed at a closed-circuit television screen looks into the robot's "brain." This is the control center for the system, and what Mobot sees, the man at the screen sees. That is the way it was the day Marvin, the "sea serpent," swam into view. Mobot gave no sign of being startled, but the man at the controls let out a yell. His teammates came to gape, too, at the 15-foot object undulating there on the screen in the glare of Mobot's headlights.

None of the observers had ever seen anything like it, nor had the experts who later viewed the pictures. There is interest in whether Marvin will bite, for one day men will join Mobot down there. Currently, there is argument as to whether the queer, undulating creature that appeared to change shape is salp, ctenophore, or siphonophore. Almost the only way to get a sure identification is to have a specimen to examine, but Marvin apparently stays down deep and has not shown himself again.

TOP: MARVIN, THE SEA SERPENT, *startled viewers of closed-circuit television screen aboard ship but did not faze Mobot. (Shell Oil Co.)*

HIGH AND DRY, *operator sees what Mobot "sees" 1,000 feet below the surface and controls activities of the mechanical diver. (Shell Oil Co.)*

An Automatic Team

Mobot will work in combination with an automatic positioning system, which automatically holds ships at sea over a fixed position with anchor and at any depth. An electronic computer which directs fore and aft propellers forms the heart of the system. Control is automatic and accurate to within 3 per cent of water depth. Conventional anchor systems grow cumbersome at 1,000-foot water depth and require many hours to install and remove. The new system cuts anchoring time to a matter of minutes.

Eureka, the core drilling ship, has drilled on as many as nine locations a day with the new technique. In use since May, 1961, this positioning system has operated effectively in 4,000 feet of water, in 20-foot waves and 40-mile winds. The system's propellers are similar to outboard motors and may be turned a full 360 degrees and controlled at variable speeds. These props hold the ship over the correct lateral and longitudinal position, and at a desired heading.

Working with Mobot, *Eureka* provides an effective method of locating and re-entering existing ocean floor wells for workover operations, where the robot would replace the tiltmeter weight, and working in unison with it,

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Threshold of Perception of Eugenol in Juvenile Sockeye Salmon

Robert M. Tarrant, Jr.

Threshold of Perception of Eugenol in Juvenile Sockeye Salmon

INTRODUCTION

To evaluate the effect of environmental changes caused by high dams on the homing capabilities of salmon, a better understanding of the mechanisms of homing behavior is needed. Hasler and Wisby (1951) theorized that homing of salmon during the later stages of migration is based on a response to the odor of the home stream. Field studies with both coho salmon (*Oncorhynchus kisutch*) (Wisby and Hasler, 1954) and chinook salmon (*O. tshawytscha*)[1] tend to support this theory. Hasler and Wisby suggested that it might be possible to condition young salmon to a synthetic odor and later attract them to this odor when they return from the ocean to spawn. Such a procedure might have useful management applications in identifying and separating stocks of migrating adults. Prior to any investigation of this possibility, information is necessary concerning levels of sensitivity to odor-producing compounds which might be used.

Eugenol was selected for study since Neurath (1949) found that the minnow

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[1] Groves, A. B., G. B. Collins, and P. S. Trefethen. Sensory factors in the homing of fall-run chinook salmon (*Oncorhynchus tshawytscha*). Manuscript in preparation.

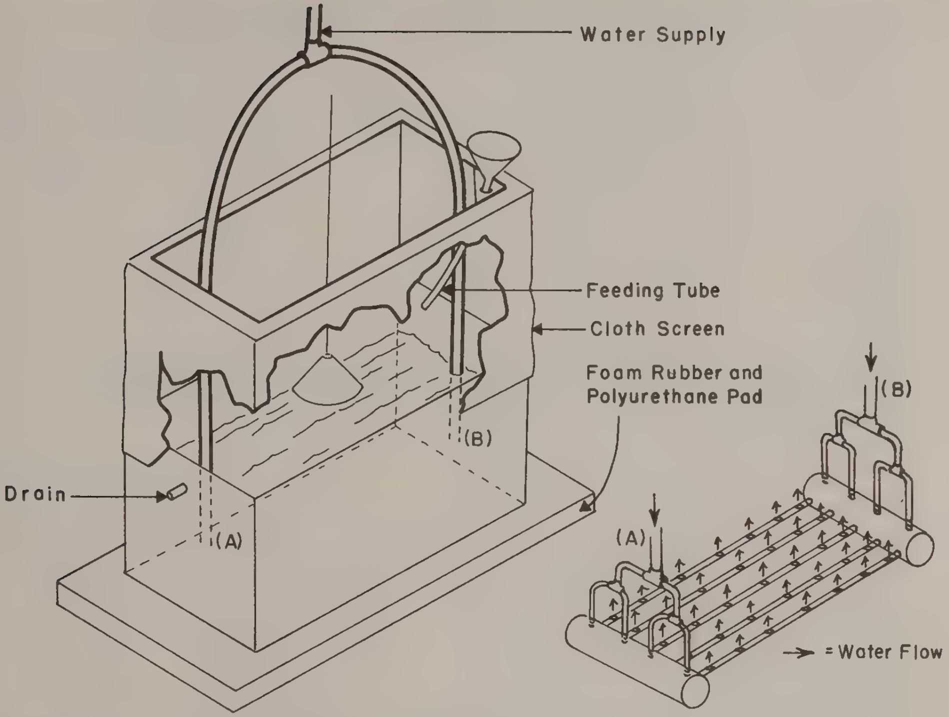

FIGURE 1.—Diagram of aquarium used for conditioning and testing juvenile sockeye salmon. A plastic water diffuser (shown on right) is located on the floor of the aquarium.

(*Phoxinus laevis*) detected this chemical by olfaction alone. The threshold of perception of eugenol was determined for juvenile sockeye salmon (*O. nerka*) in laboratory facilities at Seattle, Washington.

MATERIALS AND METHODS

One hundred sockeye salmon were obtained for the tests from the National Hatchery at Leavenworth, Washington. Before beginning the study, the fish were held 3 days in circular metal tanks flushed with dechlorinated city water. During this period they were fed dry food pellets. The fish were 1 year old and approximately 4 to 5 inches long at the beginning of the study.

A modified form of the experimental arrangement used by Tarrant (1964) was employed (Figure 1). The 77-gallon plywood aquarium was flushed with dechlorinated city water at the rate of 117 gallons per hour. Water was introduced from the bottom of the aquarium through a plastic water diffuser designed to disperse the water uniformly. Continuous illumination was provided by a 75-watt incandescent bulb 8 inches above the water surface; undetected observation of the fish was possible from a darkened area above the light.

Eugenol (only slightly soluble in water) was first dissolved in ethanol to facilitate uniform dispersal throughout the aquarium—ethanol mixes freely with both eugenol and water. Tests indicated that ethanol was not detected at the concentrations used in this study. Units of approximately 5 cc of eugenol solution were injected through a serum stopper in the water supply line with a hypodermic syringe. A solution of methylene blue was injected periodically to determine the rate of mixing within the aquarium. Mixing was complete in an average time of 34 seconds after injection.

Forty seconds after the eugenol solution

TABLE 1.—*Responses of a group of 100 juvenile sockeye salmon in tests with eugenol*[1] *and control tests with ethanol*[2]. *(Prior to the tests the fish had received 60 associations of eugenol with food)*

Concentration[3] (ppm)	Eugenol			Ethanol (Control)		
	Positive responses		Negative responses	Positive responses		Negative responses
	Number	Mean time to response[4] (seconds)	(number)	Number	Time to response (seconds)	(number)
4.50–5.00	2	35	0	0	—	1
3.50–4.00	2	35	0	—	—	—
2.50–3.00	5	35	0	1	35	3
2.00–2.40	9	44	0	0	—	1
1.50–1.90	6	48	0	0	—	1
1.00–1.40	5	60	0	0	—	1
0.50–0.90	9	81	0	0	—	1
0.36–0.40	13	113	0	0	—	1
0.30–0.34	11	115	2	0	—	3
0.24–0.28	18	114	5	1	180	6
0.16–0.22	16	128	15	0	—	12

[1] Eugenol in solution with ethanol was made up to a volume of approximately 5 cc for each test.

[2] In each control test the volume of the ethanol equaled the eugenol solution used in the succeeding test.

[3] Concentrations were decreased at each step as follows: by 0.50 ppm between 5.00 and 2.50 ppm; by 0.10 ppm between 2.50 and 0.50 ppm; and by 0.02 ppm between 0.50 and 0.16 ppm.

[4] Time was measured from injection of the chemical until the conditioned response occurred.

was injected, dry food pellets were dropped into the water through a tube above the aquarium. The fish fed actively at the water surface in the area where the food was introduced. After several associations the fish became conditioned to the chemical stimulus, which then evoked a response prior to the introduction of food. The conditioned response consisted of increased activity followed by surface-feeding behavior. Although the fish responded as a group, some individuals may have been cued by the movements of other fish.

The concentration of eugenol used in each test was calculated on the basis of the total volume of water in the aquarium. To insure complete flushing of the chemical from the aquarium, introductions were limited to one per day. The fish were subjected to 26 associations at a concentration of 2.50 ppm followed by 34 at 5.00 ppm (the concentration was strengthened to hasten conditioning). Concentrations were then lessened in successive tests until the chemical stimulus no longer evoked a conditioned response. Ethanol, in volume equal to that in the test solution, was injected as a control before several of the tests. The sequence of association and control tests was varied.

RESPONSE TO DIFFERENT CONCENTRATIONS

The conditioned response was well established within 36 associations, and after the 60th association, reduction of the concentration was begun. The fish responded to all concentrations of eugenol greater than 2.20 ppm in less than 40 seconds after injection. The time required to respond increased at lower concentrations (Table 1), and the addition of food was delayed proportionately. If no surface-feeding behavior appeared within 180 seconds after injection of the chemical, food was introduced, and the response was considered negative. At concentrations below 0.20 ppm, 240 seconds were allowed before the introduction of the food.

All concentrations of 0.32 ppm or greater evoked a positive response. The percentage of positive responses decreased rapidly at lower concentrations (Table 1). At 0.20 ppm conditioned responses were generally weaker and more delayed than at stronger concentrations. Responses at 0.18 ppm were negative with the exception of one weak positive response that appeared 200 seconds after injection of the chemical. In tests at 0.16 ppm no responses were positive, and no indication was seen that the chemical was detected.

The fish were again tested with a more concentrated solution of eugenol, which evoked a strong conditioned response. The concentration was decreased to 0.16 ppm, and the fish again failed to respond at this level. This procedure was repeated twice with identical results.

In 32 control tests with ethanol, 30 responses were negative (Table 1). The two positive responses in the control tests occurred after a period in which tests were run at approximately the same time each day for several weeks. Care was then taken to vary the time of day at which the tests were run, and no further positive control responses occurred.

Concentrations of eugenol used in the study were calculated on the basis of the total volume of water in the aquarium. Since concentrated solutions were introduced with the water supply and were dispersed throughout the aquarium, it is possible that the fish may have responded to a stronger solution than the calculated concentration. The time from injection of the chemical until the fish responded, however, always exceeded the average time required for complete mixing within the aquarium (Table 1). At 0.18 ppm the response time exceeded the time required for mixing by a factor of six.

Below 2.30 ppm the response time increased in geometric progression as the concentration of the chemical was decreased geometrically. It has long been held that as a stimulus decreases geometrically, the intensity of the sensation decreases arithmetically (Fechner's Law). Perhaps then an arithmetic decrease of sensation produced a geometric increase of response time.

EUGENOL FOR ATTRACTING RETURN MIGRANTS

The tests indicated that the perceptual threshold for eugenol in sockeye salmon of this age was no lower than 0.18 ppm. Neurath (1949), using conditioned responses, found that the threshold for eugenol in *Phoxinus laevis* was 0.06 ppm. Juvenile sockeye have been found to react to natural food extracts at 0.01 ppm (McBride et al., 1962), and young coho salmon were reported by Wisby[2] to detect morpholine at 0.000001 ppm. In these two studies a conditioned-response technique was not employed.

The relatively high threshold concentrations of eugenol required to evoke conditioned responses from juvenile sockeye would seem to limit consideration of this chemical for the purpose of conditioning young salmon and later attracting them as adults. In free-flowing streams the amount of eugenol required to approach the apparent threshold levels for sockeye would make the cost of conditioning young salmon prohibitive, but within the restriction and control of a hatchery environment its use in conditioning fish might be practical. In attracting returning migrants, much lower concentrations of eugenol might be adequate because of the reportedly acute chemical sensing ability of adult salmon (Brett and MacKinnon, 1954).

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A Pacific Polychaete in Southeastern United States

JOHN L. TAYLOR

THE marine polychaete worm *Poecilochaetus johnsoni* Hartman was originally described from a specimen taken near the mouth of Mission Bay, southern California (Hartman, 1939), and has not been previously reported from the Gulf of Mexico or the Atlantic seaboard (Hartman, 1965). This report records the occurrence of *P. johnsoni* in the southeastern United States and presents information on the biology of this rarely collected species. Specimens were collected in Florida at Seahorse Key, Tampa Bay, Naples, and Biscayne Bay in 1958-65. During the same period, the worm was also taken in North Carolina at Cape Lookout and in Core and Bogue Sounds.

EXTERNAL MORPHOLOGY

Specimens of *P. johnsoni* from southeastern United States correspond with the species description (Hartman, 1939) except for a greater variability in spinous setae and anal cirri. The original account reported three, four, or perhaps five falcate spines on the second and third setigers and described three simple and subequal cirri along the ventral border of the anus, and one on its middorsal border.

Most specimens collected in the southeast have four falcate spines on the second setiger and three on the third. Exceptions are fairly common, however, and some individuals have three to six spines on either setiger. Anal cirri usually form a ventral series of three, consisting of one median and two lateral processes. The midventral cirrus is simple, but the lateral pair may be divided distally once or several times. Only one specimen has a single middorsal cirrus; some have two dorsal cirri arising separately or jointly at a common base; and on others, the dorsal border of the anus appears plain. These features are evidently labile for eastern races of the species and do not seem of sufficient meristic importance to warrant establishment of a distinct taxonomic separation between southeastern and Pacific forms of the worm.

ECOLOGY

Environmental conditions in areas where *P. johnsoni* has been collected are summarized in Table 1. These records show that the worm commonly occurs in coastal situations having temperate or subtropical characteristics, moderate tidal flow, and a substrate of silty sand.

At most localities the mean annual salinity is above 30 o/oo and fairly stable, but at Seahorse Key, Florida, and in Bogue and Core Sounds, North Carolina, the mean value is lower and freshets periodically create brackish conditions. Although the benthic habit of *P. johnsoni* may mitigate the effects of dilute seawater, it seems likely that the worm has some capacity for osmoregulation or other physiological adjustment during periods of osmotic stress.

Marine grasses are a conspicuous feature in many areas where *P. johnsoni* occurs. The friable dwelling tube has been taken among roots and rhizomes, as well as in clear areas between patches of vegetation. In May 1965, 189 specimens were collected in a bottom sample one-half meter square, at the southern end of Core Sound, North Carolina, adjacent to Whitehurst Island, in tidal flats densely vegetated with *Zostera marina*.

Commensal pinnotherid crabs tentatively identified as juvenile *Pinnixa chaetopterana* were found in tubes of *P. johnsoni* at Seahorse Key, Florida, and Whitehurst Island, North Carolina. In both areas adult *P. chaetopterana* were collected from tubes of larger polychaetes. The small tube of *P. johnsoni* imposes a size limit on commensal crabs that can be accommodated; the association is probably temporary, providing a refuge for young crabs during early post-larval stages.

Reproduction of *P. johnsoni* apparently takes place in spring, summer, and fall when water temperature is about 20 C or above. Plankton from Tampa Bay contained larval stages of *P. johnsoni* in April, May and August (John A. Kelly, Jr., and Alexander Dragovich, unpublished). At Cape Lookout, North Carolina, a specimen taken by Lawrence McCloskey in November had ruptured median and posterior parapods, presumably damaged during release of gametes.

In comparison with other species of Poecilochaetidae (Hannerz, 1956), *P. johnsoni* has been considered most closely related to *Poecilochaetus tropicus* Okuda from the Pacific (Hartman, 1939 and 1959). From an ecological standpoint, however, *P. johnsoni* resembles in many respects the eastern Atlantic species, *Poecilochaetus serpen* Allen, studied on the English coast (Allen, 1904). The population concentration of *P. johnsoni* at Whitehurst Island, North Carolina, provides an excellent opportunity for detailed studies and clarification of the biology of this unusual and little-known spioniform polychaete.

MATERIAL EXAMINED

Seahorse Key, Florida: 2 specimens (anterior portion only), E. Lowe Pierce, coll., 1958, U. S. National Museum No. 32616; 3 specimens (anterior portion only), John L. Taylor, coll., September 22, 1960; 1 specimen (anterior portion only), John L. Taylor and Carl H. Saloman, coll., August 5, 1964.

Tampa Bay, Florida: 2 specimens (median fragments only), John L. Taylor and Carl H. Saloman, colls., August 10, 1964; 4 specimens (juvenile, meroplankton), Alexander Dragovich and John Kelly, Jr., colls., April 11, 1961, May 8, 1962, August 16, 1962 (2).

Naples, Florida: 1 specimen (anterior portion only), Charlene Long, coll., December 1958.

Biscayne Bay, Florida: 1 specimen (anterior portion only), Robert T. Paine, coll., January 26, 1960.

Cape Lookout, North Carolina: 1 specimen (anterior portion only), Lawrence McCloskey, coll., November 4, 1963.

Core Sound, North Carolina: 189 specimens (entire specimens and fragments), John L. Taylor, coll., May 4, 1965.

ACKNOWLEDGMENTS

Many people contributed to this report. Dr. Marian Pettibone, Division of Marine Worms, U. S. National Museum, identified the first specimens of *P. johnsoni* collected on the east coast of the United States. Dr. Meredith Jones, Division of Marine Worms, U. S. National Museum, reviewed the original manuscript and forwarded specimens that he identified from the collections at Naples, Biscayne Bay, and Cape Lookout. Carl Caloman, Alexander Dragovich, and John Kelly, Jr., Bureau of Commercial Fisheries Biological Station, St. Petersburg Beach, Florida, provided specimens and ecological data from the west coast of Florida. Miss Charlene Long, Museum of Comparative Zoology, Harvard University, provided field data for the Naples area. Dr. Robert Paine, Department of Zoology, University of Washington, and Durbin Tabb, Marine Laboratory, University of Miami, supplied ecological data for Bear Cut in Biscayne Bay. Mrs. Mary Kay and Lawrence Mc-

TABLE 1

Ecological conditions at points of collection of *Poecilochaetus johnsoni*

Locality	Sediment type	Ambient current (knots)	Annual range of water temperature (°C)	Salinity (o/oo)		Proximal vegetation
				Mean	Range	
Mission Bay, California	Silty-sand[1,2]	No data	10-25	34	30-35	No data
Seahorse Key, Florida	Coarse sand and shell, 2% silt and clay	0.5	10-34	25[3]	10-32	*Thalassia testudinum*
Bunces Pass, Tampa Bay, Florida	do	2[4]	12-34[3,5]	34[3,5]	33-38	do
Johns Pass, Tampa Bay, Florida	Coarse sand and shell, 11% silt and clay	1[4]	12-34[3,5]	34[3,5]	33-38	do
Naples, Florida	Silty-sand	No data	17-32[6]	33[6]	32-39	No data
Bear Cut, Biscayne Bay, Florida	Calcareous sand	1	24-30	35	35-38	*Diplanthera wrightii* *Syringodium filiforme* *Thalassia testudinum*

TABLE 1 (continued)

Ecological conditions at points of collection of *Poecilochaetus johnsoni*

Locality	Sediment type	Ambient current (knots)	Annual range of water temperature (°C)	Salinity (o/oo)		Proximal vegetation
				Mean	Range	
Cape Lookout, North Carolina	Silt deposited on living coral, *Oculina arbuscula*	1	15-28	32	30-36	No data
Whitehurst Island, Core Sound, North Carolina	Coarse sand and shell, 10% silt and clay	1	6-30	30	10-35	*Zostera marina*
Bogue Sound, North Carolina	Medium sand, 4% silt and clay	0.5[1]	6-30	30	10-35	*Diplanthera wrightii*

[1]Hartman, 1939; [2]Hartman, 1961; [3]U. S. Coast & Geodetic Survey, 1960; [4]U. S. Coast & Geodetic Survey, 1964; [5]Saloman, Finucane, and Kelly, 1964; [6]Dragovich, 1961.

Closkey, Duke University Marine Laboratory, and Hugh Porter, University of North Carolina Institute of Fisheries Research, gave notes and records for environmental conditions in Bogue Sound, Core Sound, and at Cape Lookout. Dr. John Bradshaw, Scripps Institution of Oceanography, furnished temperature and salinity records for Mission Bay, California, and vicinity.

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Visual Target Discrimination in Blacktip Sharks (*Carcharhinus melanopterus*) and Grey Sharks (*C. menisorrah*)[1]

Albert L. Tester[2] and Susumu Kato[3]

Conditioned response experiments with juvenile blacktip (*Carcharhinus melanopterus*) and grey (*C. menisorrah*) sharks (Schultz et al., 1953) were conducted at the Eniwetok Marine Biological Laboratory, Marshall Islands, during 1960. Our objective was to investigate the sharks' visual capabilities with regard to orientation, form, differential brightness, and color discrimination of targets.

The conditioned response technique has been used only recently in the investigation of sensory perception in sharks. It was employed in auditory studies by Vilstrup (1951), Kritzler and Wood (1961), Olla (1962), Davies et al. (1963), and Wisby et al. (1964), in olfactory studies by Teichmann and Teichmann (1959), in electrical sensitivity studies by Dijkgraaf and Kalmijn (1963), and in visual studies by Clark (1959, 1961, and 1963). Clark's work on instrumental conditioning of lemon sharks is particularly pertinent to the present study.

Related studies on the anatomy and physiology of the visual system of elasmobranchs (Franz, 1913 and 1931; Verrier, 1929; Gilbert, 1963) and behavioral studies in the field (Hobson, 1963) have provided some information on the visual capabilities of sharks. However, with the exception of Clark's work, subjective methods utilizing training techniques have not been used to investigate vision in sharks.

MATERIALS AND METHODS

Subjects

The sharks used were immature blacktips and greys 19 to 33 inches in total length (Table 1) captured from reef flats adjacent to the laboratory.

Experimental Apparatus

The experimental tank was located within a larger rectangular concrete tank which could be subdivided into 5-ft sections (Tester, 1963). It was housed in a building which excluded most light, and some extraneous noise. A booth adjacent to the tank enabled the observer to view the sharks through a narrow slit 5 ft above the water without being seen by them.

The design of the experimental tank is shown in Figure 1,*A*. Dimensions were: width 4 ft, length 20 ft, and depth 3 ft. The ends were rounded with curved vertical sheets of galvanized iron. Boundaries of the end compartments consisted of notches on the walls and dark lines on the bottom. All sides and ends were painted dull black, but the bottom was brown.

A 6-inch square aperture was cut in the middle of each galvanized sheet, 12 inches below the water level. For some experiments a second square was cut with its upper edge 3 inches below the bottom edge of the first aperture. Targets were mounted on panels which, guided by grooves located behind the apertures, were manipulated from the observation booth by means of cord and pulleys. In successive discrimination training, a single aperture was used. Two targets were clipped together, one above the other, and changes were made by lowering or raising the appropriate target to the level of the aperture. When two apertures were used, in simultaneous discrimination training, three targets were clipped in series, so that the middle and either the top or bottom targets were visible through the apertures.

Paired electrodes were placed along the walls of both end sections *L* and *R*. Each electrode consisted of a brass rod to which were welded nine heavy copper wires spaced 6 inches apart, extending from the surface to within 3 inches

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[3] Presently with Bureau of Commercial Fisheries, La Jolla, California.

TABLE 1

CODE NUMBER, TOTAL LENGTH, AND SEX OF BLACKTIP (B) AND GREY (G) SHARKS

NO.	LENGTH (INCHES)	LENGTH (CM)	SEX
B1	20½	52	F
B2	21	53	F
B3	23	58	M
B4	21¼	54	M
B5	32½	82	M
B6	30½	77	F
B7	22½	57	F
B8	19	48	F
G1	31	79	M
G2	33	84	F

of the bottom. Shocking was accomplished by capacitor discharge. A coupling transformer isolated the system from the 115 volt AC line. Voltage was controlled by a Variac transformer. A fullwave selenium rectifier produced DC which charged a bank of capacitors. The charge was released by a toggle switch controlling a solenoid switch, the latter with heavy contact points. A double-pole, double-throw knife switch enabled the selection of electrode pairs at either end of the tank. The best field was produced at a charge of 90 volts, the maximum rating of the capacitors.

Visual cues were made of Munsell color standards[4] on high gloss paper, possessing known values of hue (color), value (brightness), and chroma (saturation), based on the human eye in air.[5]

All targets had an area of 9 sq inches, and consisted of white (N9/) squares, circles, equilateral triangles, and rectangles (1.8 × 5 inches), grey squares with values ranging from white (N9/) to black (N1/), and colored squares with the following characteristics: red (5R5/14), yellow (5Y5/6), green (5G5/8), blue (5B5/6), and purple (5P5/9.2). All colored targets were equal to medium grey (N5/) in subjective brightness for the average human eye. The targets were glued to panels of vinyl floor tile which had been painted dull black.

Continuous illumination was provided by a fluorescent light fixture, located about 6 ft above the center of the tank with its long axis parallel to that of the tank. Similar fixtures elsewhere in the shark house contributed only slightly to the illumination, which was measured with a Weston Illumination Meter (Model 756) with Viscor filter. The remote-measurement paddle was housed in a waterproof plexiglass covering. Incident light, measured 1 inch above the water surface at various points of the tank (Figure 1,*B*), ranged from 27 to 42 ft-c. At any point, the values varied only about 1 ft-c between day and night readings. Measurements taken below the surface of the water (1, 10, and 18 inches) showed vertical gradients from 37 to 30 ft-c in the center of the middle sections, and from 24 to 22 ft-c in the center of the end sections. At the level of the targets and immediately adjacent to them, the illumination was 11 ft-c. The light and water clarity were sufficient to allow a submerged diver with a face plate to distinguish all shapes and colors of targets from one end of the tank to the other.

Training and Testing Procedure

Sharks were trained to associate selected targets with electric shock. This was accomplished by the following procedure:

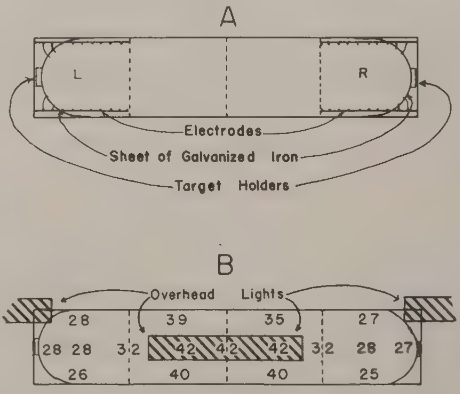

FIG. 1. *A*, Experimental tank, *B*, incident illumination one inch above the surface of the water, in foot-candles.

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[4] Munsell Color Company, Inc., 2441 North Calvert Street. Baltimore 18, Maryland, U.S.A.

[5] A complete description of the system of specifying color, with graphs for conversion to other systems, is given by the American Society for Testing Materials (ASTM Standards, Part 8, 1958).

1. The neutral targets were displayed at both ends and the shark was allowed to acclimate.

2. The negative target was displayed at one end for a period of 3 min, and the shark was shocked each time it entered that end.

3. After a rest period of 3–5 min, during which the neutral targets were displayed at both ends, the procedure was repeated at the other end of the tank.

Each training session lasted from 36 to 45 min with six alternating shocking and rest periods, or 18 min of potential exposure to shock. A minimum of 2 hr was allowed between sessions. Training was continued until a shark displayed that it had made the required association, at which time a test was conducted. If after a reasonable number of training sessions the shark had not displayed signs of discrimination, training was discontinued, usually after tests had been conducted.

During test periods the negative target was displayed but no shock was administered when the shark entered the negative end.

Both simultaneous and successive discrimination training techniques (Sutherland, 1962) were employed. In the former case two neutral targets were presented, one above the other, during rest periods, one of which was replaced by a negative target during training.

Criteria of Discrimination

Abrupt changes in behavior, when occurring consistently with appropriate target changes, were considered to be end points of behavior indicating that the shark had made the desired associations, and hence discrimination between the negative and neutral targets. The following are such behavioral changes, one or several of which occurred with individual sharks: (1) head-shaking or body-quivering on facing the negative target for the first time at the start of a training period or during a test period; (2) a sudden swirl or an abrupt change of swimming pattern on presentation of the negative target; (3) turning from the negative target before being shocked, either consistently or at least during the first few passes of each training period, or during test periods; (4) following this behavior, entering the end zone immediately after the negative target had been replaced by the neutral target; (5) sudden dashes into and out of the negative end zone immediately after the target was displayed; (6) dashing toward the negative target and abruptly turning at the line marking the entrance; (7) abrupt decrease in excitability when the target was changed to neutral, or abrupt increase in excitability when the negative target was presented.

RESULTS

Using the criteria listed above, sharks were subjectively judged to have succeeded or failed to discriminate between negative and neutral targets. Results of all experiments are summarized in Table 2; the total training time (including shocking but not control periods) and number of training sessions are entered in Table 3. In cases of positive conclusion, the times and sessions represent training until discrimination was evident. In all such cases additional training confirmed the results.

Some sharks (marked ? in Table 2) displayed good signs that they could discriminate, but their over-all behavior was too erratic to afford a firm conclusion. The implication is that further training might possibly have strengthened the association.

Behavior During Training

When a shark was shocked as it entered the end zone displaying the negative target, its body twitched noticeably. Usually it would dash away from the end compartment (escape response). Often, however, depending on the particular shark and its experience at being shocked, it would continue into the end zone despite the shock, and would turn either at the end or at some intermediate point.

During training, most sharks first developed an end association, i.e., after one or more shocks during a training period, they learned which end produced punishment and either avoided that end for the remainder of the period or, before penetrating it, displayed signs such as head-shaking which showed the end = punishment association. With most sharks, end association developed into target association with

TABLE 2

RESULTS OF DISCRIMINATION TESTS WITH BLACKTIP (B) AND GREY (G) SHARKS
(+ = discrimination; ? = probable discrimination; 0 = no discrimination;
* = simultaneous discrimination problems)

	SHARKS									
TARGETS (NEUTRAL VS. NEGATIVE)	B1	B2	B3	B4	B5	B6	B7	B8	G1	G2
No target vs. white triangle	+	—	—	—	—	—	—	—	—	—
White horizontal vs. white vertical rectangle	—	—	+	+*	+	+*	—	—	+	—
White square vs. white triangle	?	+	—	—	—	—	—	—	—	—
White circle vs. white triangle	—	—	—	0	?	—	—	—	+	—
Grey (N5/) square vs. purple square	—	—	—	—	0*	—	—	—	—	—
Grey (N5/) square vs. blue square	—	—	—	—	?*	—	—	?*	—	—
Grey (N5/) square vs. green square	—	—	0	—	—	—	—	?*	0	—
Grey (N5/) square vs. yellow square	—	—	—	—	—	—	—	+*	—	0*
Grey (N5/) square vs. red square	—	—	—	—	—	—	?	+*	—	?*
Grey (N5/) square vs. grey (N6/) square	—	—	0	—	—	—	—	—	—	—
Grey (N4/) square vs. grey (N8/) square	—	—	+	—	—	—	—	—	—	—
Grey (N4/) square vs. grey (N6/) square	—	—	+	—	—	—	—	—	—	—
Grey (N5/) square vs. grey (N8/) square	—	—	—	—	—	—	—	0*	—	+*

further training. This was shown by one or more kinds of overt responses, such as headshaking, on seeing the negative target when displayed at either end. The criteria of discrimination have already been listed.

It was expected that learning of the target = punishment association would be followed, with further training, by learning to avoid the end zone in which the negative target was displayed (avoidance response). The avoidance response was learned reasonably well (with tests showing 0–10% of the total end-zone passes into the negative end) by only two sharks in apparently simple problems: B1, no target vs. target; and B3, horizontal vs. vertical rectangles. It was not learned by other sharks trained to the rectangle orientation problem, nor by those exposed to discrimination problems involving squares, circles, triangles, colors, and shades of grey.

Prolonged training in attempts to induce the avoidance response sometimes produced behavior which might be classed as negativistic or "rebellious," e.g., with B5. This blacktip had undergone extensive training to the circle vs. triangle problem with some signs of discrimination. During rest periods, it would circle quietly in the center zone. At the start of a training period, it would make an initial shallow pass into the end displaying the negative target, turn back and enter the neutral end, and then dash into the negative end with head shaking and body quivering.

Some blacktips (but not grey sharks) had initially, or developed during training, a tendency to circle between the center zone and one end zone. This was called an "L-bias" or an "R-bias," depending on which side was favored. Two sharks (B1 and B6) showed an L-bias during shape discrimination experiments; four (B3, B5, B7, and B8) developed a strong R-bias during color discrimination experiments. The end bias could not be overcome by persistent shocking nor, in the following instance, by offering food as a reward. B6 was being trained to distinguish between horizontal and vertical rectangles but showed persistent penetration of the L-end and avoidance of the R-end. At 1845 hours, during a rest period a piece of fish was put into the R-end, upstream of L, to induce the shark to enter. It approached the R-end with seeming interest but did not enter. At 2010 hours, while being consistently shocked at L as it entered against the negative target, it suddenly dashed into the R-end, took the fish, and then dashed back into the L-end to be shocked again as it entered.

Some blacktips displayed behavior which

might be termed "nervousness," particularly in problems involving grey vs. colored targets and, to a lesser extent, in problems involving squares, circles, and triangles. This was manifested by a hypersensitivity to incidental noises which normally did not seem to affect the sharks but which, with prolonged training, caused them to make sudden dashes and quick turns. Other signs of nervous activity were: (1) apparent agitation and rapid circling, (2) prolonged figure-8 oscillations against the wall of the tank, or (3) rapid dashes from one end of the tank to the other during which the shark would turn on its back and rub the floor. This last behavior may have been related to irritation from the tag or from copepod parasites on the back which was further aggravated by body-twitching induced by shocking. A similar behavior was occasionally seen in sharks which were not being conditioned.

In most discrimination problems, the blacktips circled with increased frequency in the safe center zone as training proceeded, thus avoiding shock at either end. This circling tendency slowed the training process and in a few cases caused us to abandon training temporarily or permanently. It did not occur with the grey sharks.

There was no noticeable difference in response between sharks subject to successive and simultaneous training techniques. Each method was used in about half of the total number of test situations (Table 2).

Despite the behavioral problems discussed above, some sharks did learn to discriminate between targets. The results are presented in the sections which follow.

No Target versus Target

The one shark (B1) presented with this problem learned to associate the target (white triangle) with shock after 36 reinforcements

TABLE 3

Time (in minutes) of Training and Number of Training Sessions (in parentheses), for Blacktip (B) and Grey (G) Sharks

	SHARKS									
TARGETS (NEUTRAL VS. NEGATIVE)	B1	B2	B3	B4	B5	B6	B7	B8	G1	G2
No target vs. white triangle	36 (2)	—	—	—	—	—	—	—	—	—
White horizontal vs. white rectangle	—	—	72 (4)	158 (11)	122 (10)	72 (4)	—	—	54 (3)	—
White square vs. white triangle	360 (19)	320 (19)	—	—	—	—	—	—	—	—
White circle vs. white triangle	—	—	—	78 (5)	486 (27)	—	—	—	180 (10)	—
Grey (N5/) square vs. purple square	—	—	—	—	180 (10)	—	—	—	—	—
Grey (N5/) square vs. blue square	—	—	—	—	108 (6)	—	—	144 (9)	—	—
Grey (N5/) square vs. green square	—	—	204 (15)	—	—	—	—	255 (18)	198 (11)	—
Grey (N5/) square vs. yellow square	—	—	—	—	—	—	—	18 (1)	—	198 (11)
Grey (N5/) square vs. red square	—	—	—	—	—	—	360 (20)	89 (5)	—	210 (12)
Grey (N5/) square vs. grey (N6/) square	—	—	108 (6)	—	—	—	—	—	—	—
Grey (N4/) square vs. grey (N8/) square	—	—	108 (6)	—	—	—	—	—	—	—
Grey (N5/) square vs. grey (N8/) square	—	—	—	—	—	—	—	96 (9)	—	216 (12)

in two training sessions. Training was continued for three more days (24 sessions, 438 min) during which time B1 consistently demonstrated that it had learned the association. In addition, it also learned to avoid the negative area with almost perfect performance.

Orientation and Form Discrimination

WHITE HORIZONTAL VS. VERTICAL RECTANGLE: Discrimination of orientation of rectangles was demonstrated by all sharks, four blacktips and one grey, presented with this problem. In training sessions extending over 1–3 days, clear signs of discrimination were shown after the following number of reinforcements: B3–127; B4–365; B5–609; B6–138; G1–120. In all cases, continued training and tests provided consistent evidence that the sharks could discriminate.

Among the blacktips, B3 and B6 with the faster rates of learning were fresh sharks which had not been trained previously, whereas B4 and B5 with the slower rates had been trained unsuccessfully to the apparently difficult circle-triangle problem (see below). The grey shark, with the fastest rate of learning, had previously been trained successfully to the circle-triangle problem.

Only B3 learned to avoid the negative end. It retained the discrimination for at least 18 days without reinforcement. A gradual extinction of the association of the negative target with shock was apparent in tests conducted after 7, 12, and 18 days without reinforcement.

WHITE SQUARE VS. TRIANGLE: Two blacktips were exposed to this problem with uncertain success in one (B1) and certain success in the other (B2). Neither shark had prior training experience.

B1 showed occasional signs of discrimination after 362 reinforcements (8 sessions in 3 days), but its behavior was too erratic to afford a firm conclusion, even after an additional 11 training sessions and a total of 629 reinforcements.

An initial attempt at training B2, involving 375 reinforcements (14 sessions in 3 days), was unsuccessful. When training was resumed after 4 days of rest, a sudden and obvious development of the associatoin was apparent after 68 reinforcements (5 sessions). Continued training confirmed the positive conclusion. Tests of retention after 5 days without reinforcement were inconclusive.

WHITE CIRCLE VS. TRIANGLE: Of three sharks presented with this problem, one (B4) failed to discriminate, another (B5) showed inconsistent signs of discrimination, and the third (G1) made the discrimination.

After 103 reinforcements in 5 sessions, B4 started to swim continuously in the center zone. Training was terminated because of the persistence of this behavior.

After 727 reinforcements (17 sessions in 3 days), B5 showed some signs of discrimination. However, an additional 305 reinforcements (10 sessions in 2 days) failed to provide further evidence.

The grey shark (G1) was trained successfully to discriminate between the circle and triangle after 476 reinforcements (10 sessions in 2 days), but it did not learn the avoidance response, even after an additional 12 sessions (216 min, 380 reinforcements in 2 days).

Color Discrimination

The training of blacktips to discriminate between grey and colored squares of the same subjective brightness (to the human eye) seemed to produce more hypersensitive and erratic behavior than was displayed in other discrimination problems. It was clear that some of the subjects discriminated between the targets, but no adequate attempt was made (by substituting different shades of grey) to determine if the discrimination was based on differential brightness or hue per se.

GREY VS. PURPLE: One shark (B5) presented with this problem failed to show any sign of discrimination after 611 reinforcements during 10 sessions in 2 days.

GREY VS. BLUE: Both of two blacktips presented with this problem showed infrequent signs of discrimination, but in neither case was it possible to reach a firm conclusion.

B5 had apparently not made the discrimination after 358 reinforcements (6 sessions in 1 day). However, two tests conducted after a period of rest provided some evidence that it could distinguish between the targets.

B8 was subjected to 2 days of training during which time it received 282 reinforcements in 9 sessions. Although it showed many signs of discrimination during training periods, tests failed to verify the positive conclusion.

GREY VS. GREEN: One blacktip (B3) and a grey shark (G1) failed to discriminate this combination, but a second blacktip (B8) showed some indications of discrimination.

B3 received 299 reinforcements (15 sessions in 2 days), while G1 received 424 (11 sessions in 2 days).

B8 showed several signs of discrimination during training (18 sessions in 3 days, with 417 reinforcements). However, tests failed to confirm a positive conclusion.

GREY VS. YELLOW: A grey shark (G2) presented with this problem failed to discriminate whereas a blacktip (B8) showed clear signs of discrimination.

G2 underwent 11 training sessions in 2 days, receiving 483 reinforcements without showing any signs of learning.

B8 showed that it could discriminate from the first of 6 training sessions (total of 155 reinforcements, 99 min) conducted in 1 day, and in a test conducted the following day. The rapid rate of learning suggests that stimulus generalization had occurred. B8 had been trained to the grey-green combination prior to training against yellow.

GREY VS. RED: Of three sharks presented with this problem, a grey (G2) and a blacktip (B7) showed only inconsistent signs of discrimination, but a second blacktip (B8) definitely made the discrimination.

G2 underwent 12 training sessions in 2 days, receiving 434 reinforcements. Occasional signs of discrimination were shown during training and concluding tests, but no decision was possible because of inconsistent behavior.

After an initial 2 days of training (13 sessions, 362 reinforcements) B7 showed some signs of discrimination. However, tests failed to confirm the conclusion. An additional day of training with 166 reinforcements in 7 sessions failed to produce more definite signs of discrimination.

In contrast, B8 showed definitely that it could discriminate after 86 reinforcements in 5 sessions. An additional 6 sessions (108 min, 189 reinforcements) and concluding tests left no doubt of discrimination.

Brightness Discrimination

Experiments on differential brightness were conducted with two blacktips (B3 and B8) and one grey shark (G2). One blacktip (B3) demonstrated the ability to distinguish between shades of grey differing by 2 Munsell units, and the grey shark discriminated a difference of 3 Munsell units.

When trained to distinguish between N5/ and N6/, B3 showed no signs of discrimination after 6 sessions over 2 days (117 reinforcements). In 6 sessions of the following day (171 reinforcements) it was then successfully trained to distinguish between N4/ and N8/. A test confirmed the positive conclusion. Another test, conducted after an additional 4 training sessions (42 reinforcements) left no doubt of discrimination. When N6/ was substituted for N8/ following the last test, it was found that stimulus generalization had occurred, and B3 reacted to N6/. However, it did not respond similarly to N5/ which was also substituted for N8/, giving a difference of only 1 Munsell unit.

B8 showed no signs of discrimination between N5/ and N8/ after 9 sessions (2 days) and 196 reinforcements.

G2 showed inconsistent signs of discrimination between N5/ and N8/ during 12 training sessions in 2 days, involving 473 reinforcements. Tests confirmed that it could discriminate. Substitution of N6/ for N8/ produced some signs of discrimination, but no firm conclusion was possible.

DISCUSSION

Training Technique and Learning

The principal aim of our training technique was to induce sharks to avoid the shocking area when they had learned to discriminate the negative target, thus producing a quantitative measure of response based on the number of passes into the neutral and negative zones. In preliminary experiments conducted in 1959, some of which involved training tanks and techniques of different design, blacktips were readily trained to avoid the negative end, especially with "easy" problems, e.g., no target vs. target, and small vs. large white targets. In the results reported here, only two sharks learned the avoidance response, and only in the apparently simple problems of no target vs. target and rectangle orientation.

Difficulty in inducing avoidance may have been due partly to the lack of obvious visual cues marking the entrance to the punishment area, such as would be provided by a partition with an opening or by a barrier in a "shuttle box" such as that used by Wodinsky et al. (1962). Another factor may have been our technique of exhibiting the negative target for prolonged periods rather than single displays. Preliminary experiments indicated that the former method, although it complicated the learning process by first developing an association with the negative *end* of the tank rather than with the target itself, still resulted in faster learning of the required associations than the latter method

Another factor of considerable importance is the use of electric shock as an aversive stimulus. Church (1963) reporting upon the varied effects of punishment on behavior, points out that electric shock may elicit a variety of responses, including avoidance and aggression.

Since some subjects learned to avoid the shock in addition to discriminating the targets in simple problems, it seems likely that their failure in other problems may have been due to the fact that the problems were bordering on the threshold of the shark's visual capabilities. This may also account for the heightened activity and hypersensitivity which resulted after continued training to "difficult" problems. Such behavior occurred frequently, making it difficult to assess visual capabilities and often forcing postponement or termination of training.

There was also a suggestion that the sharks' performance may have been influenced by prior training experience. After blacktips had been trained unsuccessfully with difficult or impossible problems, they showed a relatively slow rate of learning when later presented with easier problems, e.g., orientation of rectangles.

With continued training in attempts to develop the avoidance response, some blacktips exhibited an apparent attraction for the shock. Their behavior indicated that the punishment was anticipated, and, once shocked, they often persisted in the negative zone despite repeated shocks. Best (1963) notes a somewhat similar behavior exhibited by planaria subjected to instrumental conditioning. After having demonstrated that they could make the required choice, their performance deteriorated as they chose the unrewarded alternative and became lethargic. He notes that higher animals, particularly cats, frequently exhibit such behavior, even choosing to lie on an electric grid and receive the shock rather than attempt to avoid it. He also states that "most workers agree that it may be due to overpunishment and . . . some kind of emotional response toward the entire test situation." The behavior of blacktips, and, to a lesser extent, of grey sharks, can probably be attributed to an emotional response caused by extensive punishment in training them to difficult or perhaps impossible discrimination problems.

Visual Capabilities

It has generally been assumed that the shark eye is adapted for high sensitivity rather than acuity because of its rod-rich retina, high ratio of rods to ganglion cells, and the presence of a reflecting tapetum (Gilbert, 1963). Absence of cones in vertebrate eyes is usually correlated with poor retinal resolution and colorless vision, although Walls (1942) points out the possibility that cones may not be the sole mediators of color vision. Cones have been reported to be absent in most shark retinas examined (Walls, 1942). Recently, however, Gruber et al. (1963) found for the first time some cones in a carcharhinid shark, *Negaprion brevirostris,* and in two species of *Carcharhinus* as well. In a histological study of blacktip retinas, Kato (1962) found only a single type of visual cell, presumably the rod, despite an intensive search for a second type. He also found a high ratio of visual cells to ganglion cells. A few grey shark retinas examined were similar (unpublished). Both retinas, then, are adapted for sensitivity rather than acuity. The behavior of captive sharks indicated that they could perceive small targets from a distance of at least 5 ft and sometimes at about 10 ft, supporting the histological conclusion of high sensitivity.

Regarding form discrimination, Sutherland (1962) reports that no particular difficulties in discrimination between squares, circles, and triangles have been encountered in most animals that have been tested, including octopuses, minnows, sticklebacks, pike, and a variety of higher animals. However, he points out that the angle of rotation of the figure was frequently important; for example, he found that with octopuses, a normal square (with horizontal base as in our tests) and an equilateral triangle were easier to discriminate than a diamond (square rotated through 45°) and an equilateral triangle.

Clark (1959) successfully trained two large lemon sharks (*Negraprion brevirostris*) to associate a 16 inch square white target with food. Three nurse sharks (*Ginglymostoma cirratum*), however, failed to make a strong association. Clark (1961, 1963) also trained lemon sharks to distinguish between a square and a diamond, and between a plain white square and one with vertical stripes, but was unable to train them to discriminate a square from a circle even with the large targets used.

Our blacktips and greys readily discriminated between rectangles oriented at 90° to each other. However, in other test situations involving circle vs. triangle and square vs. triangle, only two of five sharks provided positive results. The shark's difficulty in form discrimination may be attributed to poor retinal resolution, or possibly to differential ability in learning, which, in turn, may be related to our methods. Hobson (1963) suggests that form discrimination may not be utilized by grey sharks in their natural environment. In feeding tests, he found no significant discrimination between whole baitfish (suitably slit to provide good olfactory stimulation) and decharacterized baitfish (heads and fins removed).

Clark (1961, 1963) trained lemon sharks to distinguish between a white and a red circle, and a white and a red square. As in our experiments, the luminosity factor was not eliminated.

In our tests with blacktip and grey sharks, some subjects were able to distinguish, but with apparent difficulty, red and yellow, and possibly green and blue also, from grey targets. As indicated above, it still remains a question as to whether the sharks were responding to differences in brightness or to hue. The colors were chosen for maximum chroma and, to the human eye, presented a vivid contrast with grey when viewed through water. Although the illumination was somewhat low, measuring 28 ft-c at the surface and 11 ft-c at the level of the targets, there was enough light to allow color vision, at least for animals with cone-rich retinas that have demonstrated the ability to distinguish hues. For humans, 0.01 ft-c is sufficient for photopic vision (Moon, 1961). Walls (1942) reports several workers' findings that the minnow *Phoxinus laevis* matches human ability in regard to the illumination level at which they can perceive hues. John (1964), utilizing schooling responses of *Astyanax mexicanus,* found a cone threshold in the order of 0.001 ft-c.

Eyes of blacktips and greys kept in the shark house were nearly in a completely light-adapted state: the pupils were almost slits, and the tapeta were nearly completely occluded by dark pigment. It is possible that a small increase in illumination might have raised the sharks' visual ability, as it would certainly have done for animals with duplex retinas. However, optimum light conditions for blacktip and grey sharks, with all-rod retinas, may not necessarily be the same as those of animals with cone-rich retinas.

There was no noticeable difference in learning rates or ability between the simultaneous and successive techniques employed. It has been shown (Sutherland, 1962) that the former method is more advantageous if very small differences, such as neighboring shades of grey, are to be discriminated. Using the simultaneous technique, shades of grey differing by 3 Munsell units were distinguished by a grey shark but not by a blacktip. Using the successive technique, shades of grey differing by 2 Munsell units were distinguished by a second blacktip.

Difference Between Species

No consistent differences were found in the visual capabilities of blacktip and grey sharks.

However, there was a difference in their response to punishment. While undergoing training, blacktips frequently displayed hypersensitive and erratic behavior, while grey sharks did not deviate much from their normal swimming pattern. This may reflect a real difference in normal behavior. Hobson (1963) found that blacktips were much more wary than grey sharks in their natural environment.

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THE SKIPJACK TUNA FISHERY IN HAWAII[1]

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ABSTRACT

Skipjack tuna (Katsuwonus pelamis) is the major commercial species in the fisheries of Hawaii, contributing about two-thirds by weight to the total marine catch of fish and shellfish, and accounting for about 40 percent of the total annual ex-vessel value. In recent years, the catch has averaged 9.6 million pounds (5,280 metric tons). Skipjack tuna are caught by pole and line. The nehu (Stolephorus purpureus), an anchovy, constitutes about 92 percent of the bait used. The fishing sampans range from 58.3 to 80.5 feet long. Catches vary considerably not only during the year (the peak is in midsummer), but from year to year. About 75 percent of the catch is made within 20 miles of the main islands. In order to standardize statistics on effort, the vessels were placed in two categories, according to capacity of the baitwell (which roughly corresponds to the size of the vessels). In 1952-64 the catch per standard effective trip (i.e., the number of pounds per trip taken by the average larger vessel) ranged from 4,737 pounds in 1952 to 7,119 pounds in 1959. Fishing intensity was higher in the early 1950's than it is today.

INTRODUCTION

Skipjack tuna Katsuwonus pelamis (Linnaeus), or aku as it is called locally, long has been the major commercial species in the fisheries of the Hawaiian Islands; it contributes about two-thirds by weight to the total Hawaiian marine catch of fish and shellfish, and accounts for about 40 percent of the total annual ex-vessel value. In 1928-36, the average annual catch of skipjack tuna was about 5.2 million pounds. The catch then increased sharply and, from 1937 to 1940, averaged 11.1 million pounds. Fishing ceased in World War II. In recent years, the catches have fluctuated widely; in 1952-64, catches were as low as 6.1 million and as high as 14.0 million pounds and averaged 9.6 million pounds.

Because the catch of skipjack tuna represents a large proportion of the islands' fish catch, the causes of fluctuations in abundance are of great interest to the fishermen. The objectives of this study are to describe the trends in catches, in effort, in catch per unit effort, and to examine the fluctuations in abundance of skipjack tuna in relation to the pressure of fishing.

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[1] Much of the material contained in this paper was extracted from Uchida, in press.

DESCRIPTION OF THE FISHERY

The present brief description of the fishery is based on June (1951).

Fishing Operations

In Hawaii, skipjack tuna is caught exclusively with pole and line and live bait. Fishing is usually confined to waters within 90 miles of the main islands. The vessels leave for the fishing grounds before dawn and start to scout and fish when daylight comes. The presence of skipjack tuna on the fishing ground is indicated to the fishermen almost exclusively by birds, flocks of which are often associated with schools of fish. When fish are sighted, the vessel attempts to reach the head of the school; water sprays are then turned on and the chummer starts to scatter live bait into the water. If the fish begin to bite, the fishermen stand along the stern to fish. Fishing continues until the captain decides that further fishing is not worth while. If chumming is unsuccessful, the school is abandoned and scouting is resumed.

The vessels may encounter several schools of skipjack tuna during the day, but the fish may bite in only about half of the schools. Scouting and fishing are discontinued as darkness approaches, and the vessels usually head for port to unload the day's catch.

To determine compensation the cost of fuel and ice is first deducted. The balance is divided between the owner of the vessel and the crew from the gross receipts--37 percent to the owner and 63 percent to the crew. Captains and engineers usually receive a 10 and 5 percent bonus, respectively, from the owner's share. The cost of the food is subtracted from the crew's share.

Bait and Baiting Areas

The nehu or anchovy Stolephorus purpureus Fowler, makes up about 92 percent of the bait used in skipjack tuna fishing (Yamashita, 1958). Another bait, of minor importance, is the iao or silverside, Pranesus insularum (Jordan and Evermann). Each vessel catches its own bait, fishing night and day until a sufficient supply is obtained. The principal bait fishing grounds on the island of Oahu are Kaneohe Bay and Pearl Harbor, which supply the bulk of the catch, and Honolulu Harbor. On Maui, the principal baiting grounds are Maalaea Bay and the Kihei region. Oahu and Maui are the major sources of nehu. Largely because of the limited extent of the baiting grounds, Hawaii, Kauai, and Molokai contribute only small amounts of bait.

The Aku Sampans

The aku sampans are generally built of wood, and range from 58.3 to 80.5 feet in registered length and from 27 to 77 gross tons. These vessels carry from 6 to 14 men per fishing trip. Each vessel is equipped with six baitwells arranged on the afterdeck in parallel rows of three. Emptied of bait during fishing, these baitwells provide stowage for the catch.

Since the larger crews give the larger vessels greater fishing power, the size of a vessel influences its potential efficiency as a fishing unit in a pole-and-line fishery. The number of men aboard per trip varies among vessels and with the years. To reduce the effects of this variability upon catch statistics, I have separated the vessels of the fleet into two size classes. Because the vessel's bait-carrying capacity reflects its fish-carrying capacity, this characteristic was used to separate the vessels into two sizes--small and large. Vessels with bait-carrying capacities of less than 800 gallons per baitwell were called small and designated as Class 1; those with capacities greater than 800 gallons per baitwell were called large and designated as Class 2.

In recent years, more vessels with large bait-carrying capacities have been built. Figure 1 shows the year of construction of the vessels plotted against their bait-carrying capacity (expressed as average effective volume per baitwell). Of 17 vessels built before World War II, 14 had capacities of less than 800 gallons per baitwell. In the immediate postwar period, new vessels had a large bait-carrying capacity; of 11 vessels built in 1946-55, 10 had capacities of more than 800 gallons per baitwell. Almost all of the vessels lost or withdrawn from the fleet in recent years were of the older Class 1 type.

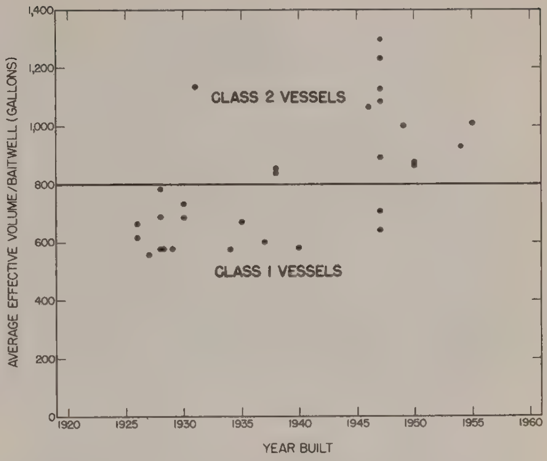


Figure 1.--Average effective volume per baitwell of Hawaiian skipjack tuna vessels plotted against the date of construction. The 800-gallon level is the dividing line for the size classes of vessels.

TRENDS IN CATCHES OF SKIPJACK TUNA

Catches of skipjack tuna in Hawaii vary considerably not only during the year, but also from year to year. Trends in monthly and annual catches and in inshore-offshore catches are briefly discussed in the following section.

Monthly Catches

The seasonal character of the Hawaiian skipjack tuna fishery is shown by the monthly catches averaged over the 13-year period, 1952-64, (table 1 and fig. 2). Usually the smallest catches

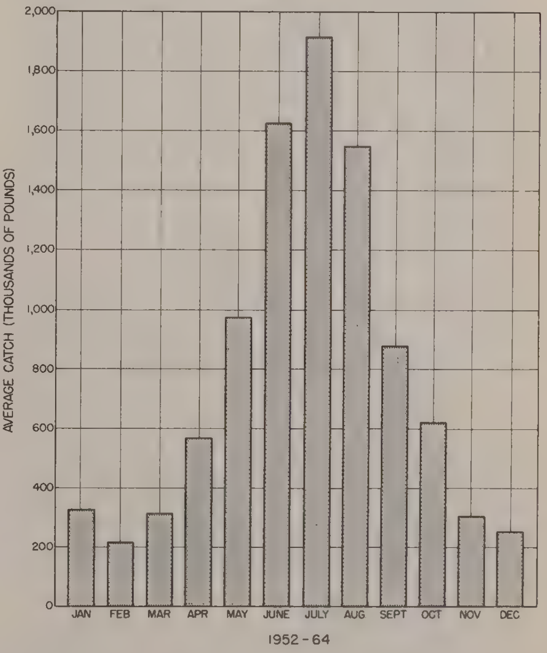


Figure 2.--Average monthly catch of skipjack tuna, 1952-64.

Table 1.--Monthly and annual catches (thousands of pounds) of skipjack tuna in Hawaii, 1952-64

Month	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	Average
Jan.	29	200	271	98	322	524	638	215	242	492	459	293	497	329
Feb.	90	204	185	118	281	133	236	107	179	247	412	337	277	216
Mar.	56	576	359	263	230	454	151	397	327	600	199	156	350	317
Apr.	387	864	759	681	433	331	792	839	411	620	480	191	627	570
May	578	1,240	1,132	1,399	1,375	816	277	1,757	842	930	1,178	574	558	974
June	818	2,241	2,804	2,197	1,926	812	948	1,679	776	2,721	2,308	1,125	803	1,628
July	1,654	1,510	3,705	1,824	2,321	919	1,405	2,382	1,430	2,288	1,809	1,641	2,060	1,919
Aug.	1,758	2,142	2,178	1,170	1,586	698	1,191	1,815	1,396	1,359	922	2,331	1,587	1,549
Sept.	987	1,281	1,049	993	1,055	489	631	1,377	690	705	568	620	993	880
Oct.	576	1,199	1,121	440	725	530	186	1,064	439	516	525	395	402	624
Nov.	110	218	390	272	635	282	144	626	219	213	170	291	436	308
Dec.	249	384	68	239	243	142	235	155	409	203	385	145	434	253
Total	7,292	12,059	14,021	9,694	11,132	6,130	6,834	12,413	7,360	10,894	9,415	8,099	9,024	9,567

Table 2.--The total annual marine catches (thousands of pounds) and values (thousands of dollars) of fish and shellfish and of skipjack tuna, Hawaii, 1952-64

Year	Fish and shellfish		Skipjack tuna	
	Marine catch	Value	Catch	Value
1952	13,890	3,427	7,292	1,063
1953	18,798	3,758	12,059	1,594
1954	20,523	3,653	14,021	1,761
1955	14,989	3,044	9,694	1,065
1956	16,420	3,092	11,132	1,262
1957	10,616	2,534	6,130	794
1958	11,266	2,569	6,834	899
1959	16,476	3,121	12,413	1,475
1960	11,061	2,662	7,360	1,001
1961	14,401	2,839	10,894	1,307
1962	13,104	2,775	9,415	1,174
1963	11,708	2,648	8,099	1,090
1964	12,652	2,813	9,024	1,222

Table 3.--The estimated inshore and offshore catches (thousands of pounds) of skipjack tuna in the Hawaiian fishery, 1952-64

Year	Inshore catch	Offshore catch
1952	5,542	1,750
1953	7,959	4,100
1954	8,833	5,188
1955	8,046	1,648
1956	8,126	3,006
1957	4,904	1,226
1958	5,877	957
1959	10,303	2,110
1960	6,624	736
1961	8,497	2,397
1962	7,720	1,695
1963	5,750	2,349
1964	6,136	2,888
Average	7,255	2,312

are made in February. The catch increases gradually from about April. Progressively larger catches are made in May and June, peak catches in July, and high catches in August; from September the catch declines to a low level in December. May through September are usually considered the season months for skipjack tuna in Hawaiian waters.

Annual Catches

The annual catches of skipjack tuna vary widely (table 2). In 1952-64, the average total annual catch was about 9.6 million pounds and the average value was about $1.2 million. The catches were considerably below average in 1952, 1957, 1958, 1960, and 1963. Particularly significant were the 1957-58 catches, because in these years the value of the catch declined so drastically that several of the marginal producers had to quit fishing. In contrast, fishing has been exceptional in some years. For example, the catches in 1953, 1954, and 1959 averaged 12.8 million pounds and had an average value of $1.6 million.

Inshore and Offshore Catches

About 75 percent of the skipjack tuna catch in Hawaii is made within 20 miles of the main islands (inshore area). In 1952-64, the percentage of the catch in this inshore area ranged from 63 percent in 1954 to 90 percent in 1960. Table 3 gives the estimated inshore and offshore catches. In a good fishing year such as 1959, the inshore area alone produced 10.3 million pounds, which was considerably more than the total annual catch from both areas in some other years. The offshore catch increased from about 1.8 million pounds in 1952 to a peak of about 5.8 million pounds in 1954. After a sharp decline to about 1.6 million pounds the following year, the offshore catches fluctuated between 0.8 and 3.0 million pounds from 1956 to 1964 (fig. 3).

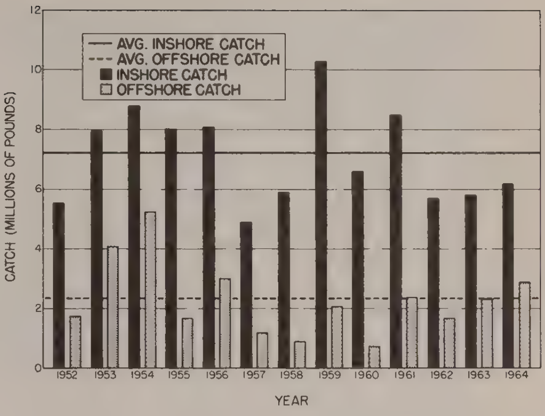


Figure 3.--The estimated inshore and offshore catches of skipjack tuna in the Hawaiian fishery, 1952-64.

FISHING EFFORT

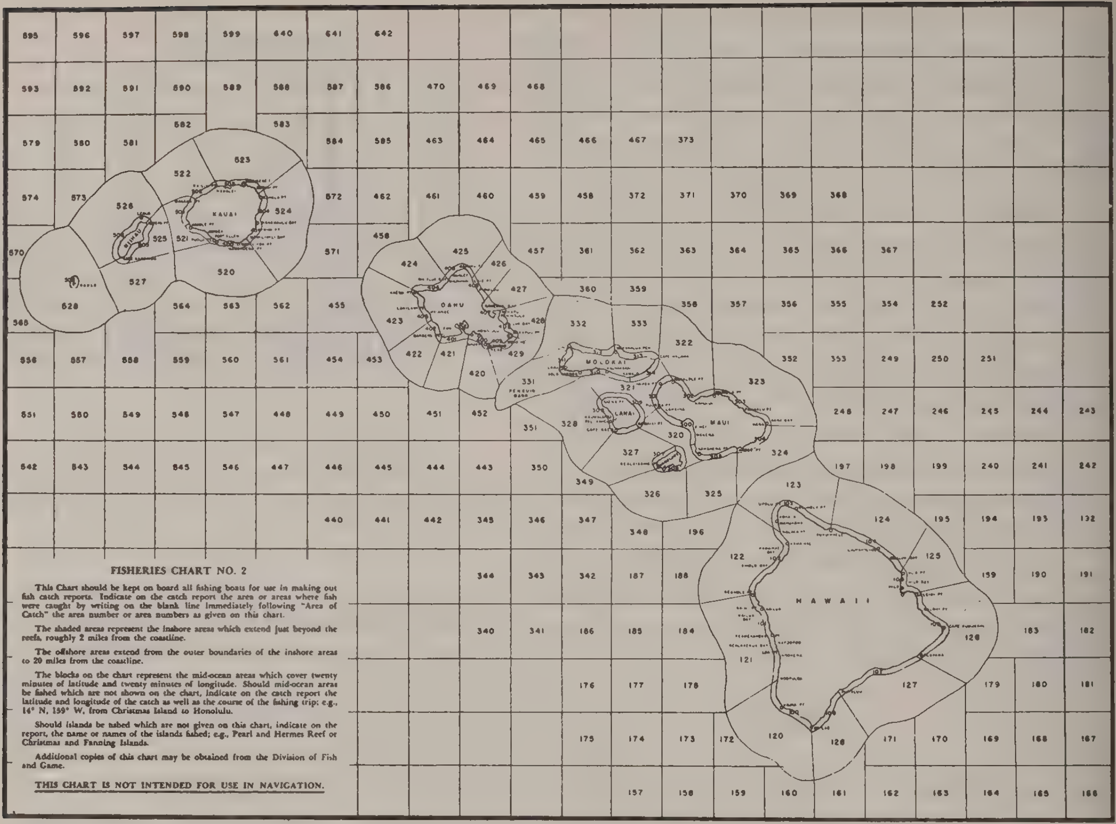
Fishing effort of a unit of fishing gear is the product of its fishing power and the number of times or duration of its use. For example, a trip of an aku sampan that carries a certain number of crewmen and scouts and fishes for a certain length of time may be considered a unit of fishing effort. To understand the relation between catch and effort in the Hawaiian skipjack tuna fishery, it is essential to define effort precisely.

Effective Trip as a Measure of Fishing Effort

Before July 1964, the Aku Catch Reports, which the fishermen filled out and sent in to the Hawaii Division of Fish and Game, made no provisions for recording zero-catch trips. Consequently, a fisherman reported only the number of the statistical area in which he fished (fig. 4) and the amount of aku caught from that area when he had a successful trip, and made no entry when he failed to make a catch. For this report, therefore, I use a trip in which skipjack tuna were caught as the unit of fishing effort and call it an effective trip. It usually represents 1 day's fishing. Because zero-catch trips were not recorded in the past, the unit of effort used in this report is always an underestimate. The extent of the underestimate may not be serious in years when fishing is good and zero-catch trips are infrequent (Shippen, 1961), but may be large in years when fishing is poor and zero-catch trips are numerous.

Estimates of Zero-Catch Trips

To learn the extent of zero-catch trips in the skipjack tuna fishery of Hawaii, logbook records collected from several selected vessels in 1957-59 were examined. Both 1957 and 1958 were poor years (catches less than 7 million pounds), whereas 1959 was a good year (catch about 12.4 million pounds).



FISHERIES CHART NO. 2

This Chart should be kept on board all fishing boats for use in making out fish catch reports. Indicate on the catch report the area or areas where fish were caught by writing on the blank line immediately following "Area of Catch" the area number or area numbers as given on this chart.

The shaded areas represent the inshore areas which extend just beyond the reefs, roughly 2 miles from the coastline.

The offshore areas extend from the outer boundaries of the inshore areas to 20 miles from the coastline.

The blocks on the chart represent the mid-ocean areas which cover twenty minutes of latitude and twenty minutes of longitude. Should mid-ocean areas be fished which are not shown on the chart, indicate on the catch report the latitude and longitude of the catch as well as the course of the fishing trip: e.g., 14° N, 159° W, from Christmas Island to Honolulu.

Should islands be fished which are not given on this chart, indicate on the report, the name or names of the islands fished; e.g., Pearl and Hermes Reef or Christmas and Fanning Islands.

Additional copies of this chart may be obtained from the Division of Fish and Game.

THIS CHART IS NOT INTENDED FOR USE IN NAVIGATION.

Figure 4.--Hawaii Division of Fish and Game Fisheries Chart No. 2, which shows the statistical areas established for Hawaiian waters.

Zero-catch trips were more frequent among Class 2 than among Class 1 vessels. The higher rate of occurrence in poor years (1957-58) than in the good year (1959) indicates a tendency for the percentage of zero-catch trips to decrease as total catch increases. From the data for these selected vessels, the total number of zero-catch trips for the entire fishing fleet was estimated for these years. In 1957, a total of 1,578 effective trips was reported by both size classes of vessels, but the estimated total number of unreported zero-catch trips was estimated to be 822, or an average of about 33 per vessel. The number of zero-catch trips in 1958 was estimated to be about 502, considerably less than in 1957; the average per vessel for the year was about 21. In 1959, a good year in the fishery, the estimated number of zero-catch trips for the fleet was only 128--about 6 per vessel.

These results indicate that catch per effective trip should be interpreted with caution. Effective effort underestimates fishing pressure, but it has been used because information on zero-catch trips was not available from the catch reports used. This shortcoming has been remedied; in July 1964, the Hawaii Division of Fish and Game issued revised catch report forms that have spaces for recording zero-catch trips.

Average Number of Men Hooking per Effective Trip

The number of men hooking per trip has a directly proportionate effect on catch. It is, therefore, important to examine the year-to-year variation in this number.

The average number of men hooking per effective trip on Class 1 and Class 2 vessels in 1950-60 is given in table 4 and is shown graphically in figure 5. In general the annual average number of men hooking per effective trip declined. Among Class 1 vessels, the average was fairly steady from 1950 to 1955, then dropped and remained at a lower level in 1956-60. The average for Class 2 vessels declined almost steadily from 1950 to 1960.

The primary reason for this decline is the failure of the fishing industry to attract new fishermen to replace those that have retired or have quit fishing. This decline in the number of fishermen has paralleled the decline in the number of vessels fishing.

Table 4.--The annual average number of men hooking per effective trip on Class 1 and Class 2 vessels, 1950-60

Year	Class 1 vessels	Class 2 vessels
1950	8.4	10.4
1951	8.2	9.6
1952	8.4	9.2
1953	8.6	9.7
1954	9.2	9.8
1955	8.9	8.3
1956	7.1	8.7
1957	6.7	7.4
1958	7.1	8.1
1959	7.6	7.2
1960	6.9	7.4

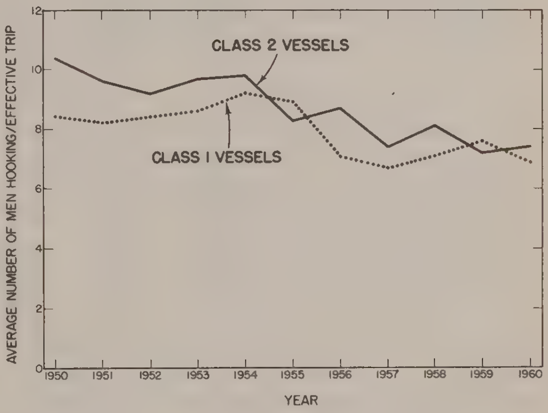


Figure 5.--Annual average number of men hooking per effective trip on Class 1 and Class 2 vessels, 1950-60.

Distribution of Effort by Areas

About 80 percent of the effective trips during any given year were in the inshore area (table 5). The percentage of effective inshore trips for both size classes of vessels, shown in figure 6, declined from 1952 to 1954, but then increased gradually. With the exception of 1954 and 1963, the percentage of effective inshore trips of Class 1 and Class 2 vessels did not differ greatly. Over the 13-year period, the percentage of inshore trips averaged about 83 percent for both Class 1 and Class 2 vessels.

Since a larger percentage of the total trips was made within 20 miles of land, and the total catch from the inshore area far exceeded that from the offshore area, one may wonder if skipjack tuna are more abundant inshore. Survey cruises in 1953 indicated that tuna schools were equally numerous offshore and inshore except for sectors to the

Table 5.--The number and (in parentheses) percentage of effective trips in the inshore and offshore areas, the total number of effective trips, and the average number of effective trips per vessel by Class 1 and Class 2 vessels, 1952-64

Year	Class 1 vessels					Class 2 vessels				
	Number of vessels	Number of effective trips				Number of vessels	Number of effective trips			
		Inshore	Offshore	Total	Average per vessel		Inshore	Offshore	Total	Average per vessel
1952	16	658 (77)	197 (23)	855	53	12	555 (80)	137 (20)	692	58
1953	16	799 (72)	308 (28)	1,107	69	11	738 (76)	232 (24)	970	88
1954	15	696 (70)	291 (30)	987	66	12	690 (77)	209 (23)	899	75
1955	14	817 (88)	116 (12)	933	67	14	748 (86)	124 (14)	872	62
1956	13	709 (76)	222 (24)	931	72	13	772 (81)	184 (19)	956	74
1957	13	540 (81)	128 (19)	668	51	12	742 (82)	168 (18)	910	76
1958	11	587 (89)	72 (11)	659	60	13	783 (90)	82 (10)	865	66
1959	8	658 (84)	121 (16)	779	97	13	884 (84)	171 (16)	1,055	81
1960	8	563 (92)	51 (8)	614	77	13	858 (92)	73 (8)	931	72
1961	8	608 (87)	88 (13)	696	87	13	939 (84)	179 (16)	1,118	86
1962	8	646 (89)	80 (11)	726	91	12	804 (86)	131 (14)	935	78
1963	8	727 (90)	80 (10)	807	101	12	711 (77)	213 (23)	924	77
1964	8	659 (79)	171 (21)	836	104	12	850 (76)	267 (24)	1,117	93

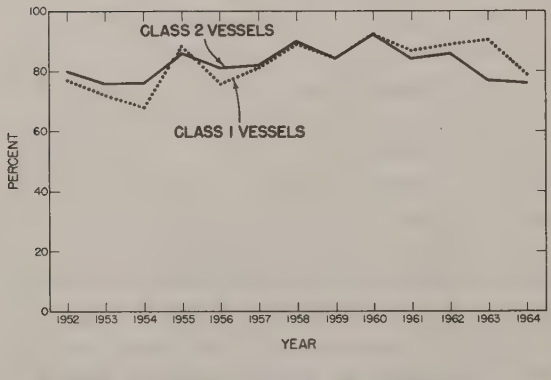


Figure 6.--Percentage of effective inshore trips by Class 1 and Class 2 vessels, 1952-64.

northeast and southwest of Oahu; there the presence of schools appeared to be seasonal.

If schools are equally abundant offshore and inshore, the question arises why effort has been concentrated in the inshore fishing grounds. It is likely that fishermen reduce costs by remaining near port as long as they can make profitable catches. The concentration of effort inshore also may be dictated by the quality and quantity of live bait. Even though it may occasionally survive as long as a week, the delicate nehu may die within a few hours. The fishermen logically would fish inshore to use the bait quickly before heavy mortality occurs. Furthermore, the need to replenish live-bait supplies to some extent restricts trips to the distant offshore grounds.

Average Number of Effective Trips per Vessel per Year

The average number of effective trips per vessel per year varied widely in 1952-64 (table 5). The average number of effective trips per Class 1 vessel per year (fig. 7) fluctuated between 51 and 72 in 1952-58, rose sharply to 97 in 1959, dropped to 77 in 1960, and increased steadily from 87 to 104 in 1961-64. Among Class 2 vessels, the average rose very sharply from 58 to 88 in 1952-53, then declined to 75 in 1954 and to 62 in 1955. After 1955, the average increased gradually, reaching a maximum of 93 in 1964.

The increase in the number of effective trips is perhaps a function of the availability of bait. As the number of Class 1 vessels declined, the remaining vessels experienced less competition for bait and were able to obtain sufficient amounts for additional trips.

CATCH PER EFFORT

In research that deals with fish populations, it is often desirable to have some index that is proportional to stock density. Catch per effort is nearly always the best available, although it is rarely exactly proportional to stock density.

In the sections that follow are discussions on catch per boat-month and catch per effective trip with comments on their shortcomings as indices. An index that is superior to these is catch per standard effective trip; it is based on a standardized unit of effort that takes into account differences in fishing power among the aku sampans.

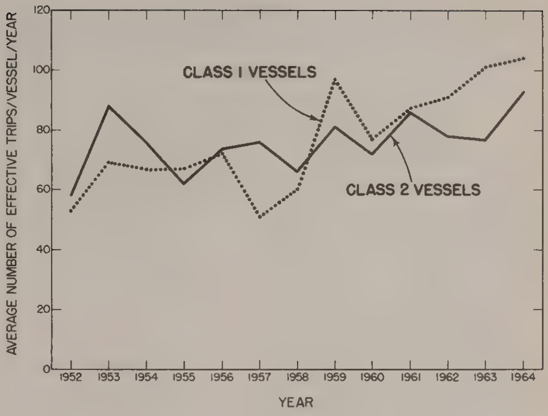


Figure 7.--Average number of effective trips per vessel per year by Class 1 and Class 2 vessels, 1952-64.

Catch per Boat-Month

The catch per boat-month is an index that tells us the average number of pounds of skipjack tuna caught per boat per month. These averages are given in table 6 and are shown in figure 8 in relation to the total catch.

The fluctuations of the catch per boat-month were similar to those of the total catch. In 1952-64, the catch per boat-month among Class 1 vessels was as low as 20,400 pounds and as high as 45,300 pounds. The average over the 13-year period was about 31,700 pounds. Among Class 2 vessels, the catch per boat-month ranged from 28,400 pounds to 55,100 pounds and averaged 41,700 pounds.

The curves for both Class 1 and Class 2 vessels show an upward trend, whereas the curve of the total catch does not. This upward trend in the catch per boat-month is primarily due to the increase in the number of trips made per vessel per year. Earlier, it was shown that both Class 1 and Class 2

Table 6.--The total catch, number of boat-months, and catch per boat-month of Class 1 and Class 2 vessels, Hawaii, 1952-64
[Catches are in thousands of pounds]

Year	Class 1 vessels			Class 2 vessels		
	Total catch	Number of boat-months	Catch per boat-month	Total catch	Number of boat-months	Catch per boat-month
1952	3,094	148	20.9	3,183	112	28.4
1953	5,192	150	34.6	5,352	117	45.7
1954	4,949	151	32.8	6,280	120	52.3
1955	3,735	145	25.8	4,522	134	33.7
1956	4,891	139	35.2	6,046	136	44.4
1957	2,223	109	20.4	3,851	132	29.2
1958	2,255	96	23.5	4,239	132	32.1
1959	4,170	92	45.3	7,775	141	55.1
1960	2,281	87	26.2	4,825	127	38.0
1961	3,474	90	38.6	7,305	136	53.7
1962	3,082	84	36.7	5,004	121	41.4
1963	2,782	86	32.3	5,139	120	42.8
1964	3,310	82	40.4	5,640	125	45.1

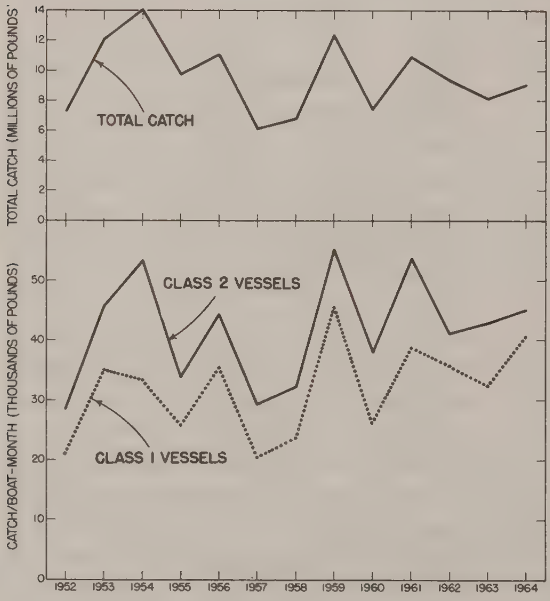


Figure 8.--The total catch and the catch per boat-month of Class 1 and Class 2 vessels, 1952-64.

vessels made more trips in recent years. Before 1959, Class 1 and Class 2 vessels averaged about 62 and 71 effective trips, respectively, per vessel per year, whereas in 1959-64, they averaged 93 and 81 trips per vessel per year.

Catch per Effective Trip

The catch of skipjack tuna per effective trip, given in table 7, is an index of the success of fishing. Figure 9 shows this index plotted by size classes of vessel and by areas. The curve of the inshore catch per effective trip for Class 1 vessels fluctuated within a relatively narrow range, from 3,219 to 5,133 pounds, whereas the curve for offshore fishing fluctuated more widely, from 3,728 to 7,758 pounds. Among Class 2 vessels, the catch per effective trip ranged from 4,210 to 7,416 pounds in the inshore area, whereas offshore catches averaged 4,333 to 9,909 pounds.

The catch per effective trip was larger in the offshore than in the inshore area every year except in 1959, when the inshore catches of Class 2 vessels averaged slightly higher than offshore catches. Furthermore, the average catches of Class 2 vessels were consistently larger than those of Class 1 vessels in both the inshore and offshore areas.

Since the average number of men hooking declined from 1950 to 1960, one would expect a similar decline in the catch per effective trip. No decline appears, however, in figure 9. Several factors seem to have been responsible for preventing this expected decline in the catch per effective trip.

The greatest effect on the catch per effective trip has been made by a change in fishing technique. In the past, when a fisherman caught a fish, he grasped it under his arm so that he could remove the barbless hook; he then dropped the fish on the deck. (Among local fishermen, the method is called ''catch'' or its Japanese equivalent ''daku,'' which means to hold in one's arm.) A considerable amount of practice and experience is required before one develops the skill necessary to fish by this method. Another method used only occasionally in the past was flipping, in which the fisherman swings the fish aboard and suddenly relaxes the tension on the pole to permit the hook to fall clear of the fish's mouth. (This method is sometimes called ''mochikomu,'' which in Japanese means to bring in.) The fishermen say that flipping allows them to catch fish faster and does not require the same degree of skill as does catching fish under the arm, but tires them more rapidly. The shift in emphasis from catching under the arm to flipping permitted a short-handed crew of limited experience to equal or better the catch of a larger and more experienced group of fishermen. Because flipping tends to bruise the fish, some fishermen still catch them under the arm when fishing the large skipjack tuna which bring a premium price on the fresh fish market. Bruised fish bring lower prices.

Table 7.--The catch (pounds) per effective trip of Class 1 and Class 2 vessels in the inshore and offshore areas of the Hawaiian fishery, 1952-64

Year	Class 1 vessels		Class 2 vessels	
	Inshore	Offshore	Inshore	Offshore
1952	3,586	3,728	4,323	5,722
1953	4,055	6,337	5,069	6,943
1954	3,867	7,758	6,312	9,210
1955	3,762	5,704	5,048	6,023
1956	4,914	6,338	5,871	8,228
1957	3,219	3,790	4,210	4,333
1958	3,238	4,928	4,723	6,593
1959	5,133	6,551	7,416	7,129
1960	3,573	5,283	5,093	6,244
1961	4,775	6,490	5,891	9,909
1962	4,019	6,071	6,066	8,602
1963	3,259	5,151	4,572	8,867
1964	3,671	5,031	4,338	7,313

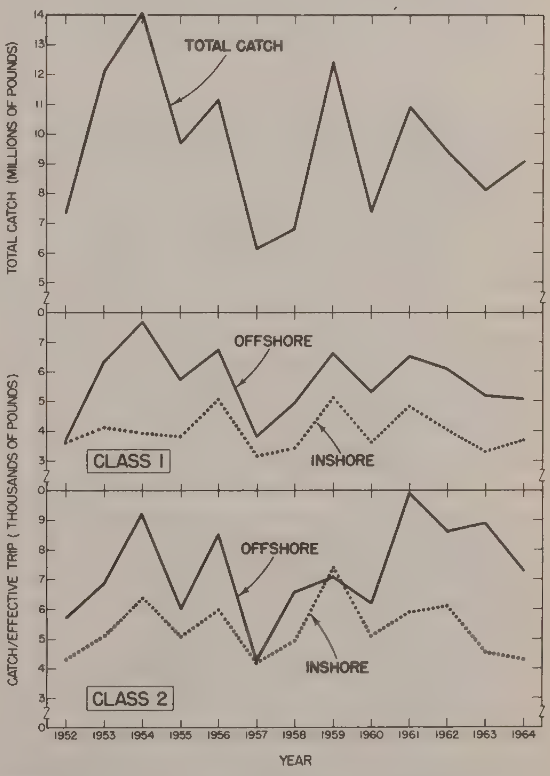


Figure 9.--Total catch and catch per effective trip by areas for Class 1 and Class 2 vessels, 1952-64.

Another factor that affected the catch per effective trip was the decrease in the number of vessels fishing, particularly among Class 1 vessels. Fishing efficiency per vessel increases when vessels that do poorly in the fishery are forced to stop fishing. In 1952-64, the number of Class 1 vessels actively fishing decreased from 16 to 8 (2 were wrecked and 6 stopped fishing). Ranking of Class 1 vessels according to the total catch of each vessel showed that the eight vessels fishing in 1964 were usually among those that were ranked high in previous years. As those that did poorly in the fishery stopped fishing, the fishing efficiency, as measured by the average catch per effective trip of all the remaining vessels, increased.

Catch per Standard Effective Trip

Data on catch per effort are frequently interpreted as indicating the apparent abundance of the fish on the fishing ground. They should, however, be regarded with caution since the values are of relative rather than absolute significance in comparisons of one year with the next.

Differences between the large and small vessels in numbers of men and in quantity of bait carried and hence in catching ability can complicate the estimates of apparent abundance. Rather than analyze the data for the two classes of vessels separately, I have employed only one index, which is based on a ''standard'' unit of fishing effort. This unit is derived from a set of efficiency factors that translate unequal skills, gears, and fishing practices and capacities into a standard unit. For example, under conditions of equal abundance, when a small vessel makes a smaller catch than a large vessel, standardization of the effort units takes into account the differences in their fishing power.

The effective trips of Class 2 vessels were selected as the standard unit of fishing effort and all Class 1 trips were converted to an equivalent number of Class 2 trips. The calculated total number of Class 2 trips (standard effective trips) was called the fishing intensity. The total catch, the catch per standard effective trip, and fishing intensity are given in table 8 and are plotted in figure 10.

The catch per standard effective trip was at 4,737 pounds in 1952, rose in 1953 and again in 1954 to reach a peak of 6,983 pounds, then dropped to about the 1952 level in 1955. Another peak in 1956 was followed by a decline to the lowest level in 1957. The catch per standard effective trip reached another peak in 1959, exceeding that of 1954, then declined in 1960. It rose to about the 1956 level in 1961 and since then has shown a steady decrease to 1964. This index had no trend; rather, the values

Table 8.--Total catch (thousands of pounds) of skipjack tuna in Hawaii, catch per standard effective trip (pounds per Class 2 trip), and fishing intensity (in Class 2 trips), 1952-64

Year	Catch	Catch per trip	Intensity
1952	7,292	4,737	1,539
1953	12,059	5,486	2,198
1954	14,021	6,983	2,008
1955	9,694	4,986	1,944
1956	11,132	6,430	1,731
1957	6,130	4,166	1,471
1958	6,834	4,850	1,409
1959	12,413	7,119	1,744
1960	7,360	5,062	1,454
1961	10,894	6,629	1,643
1962	9,415	6,358	1,481
1963	8,099	5,500	1,473
1964	9,024	5,108	1,766

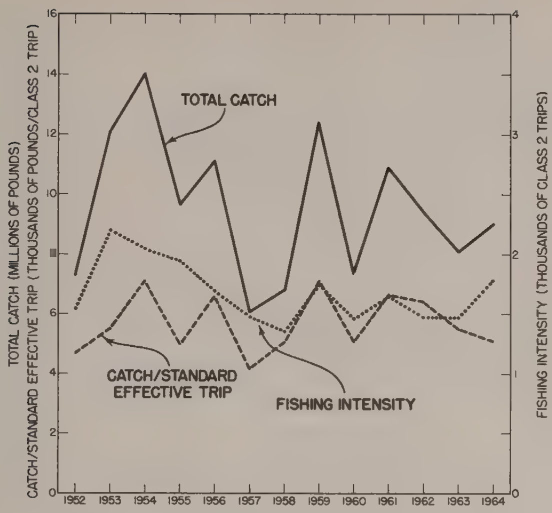


Figure 10.--Total catch, catch per standard effective trip, and fishing intensity for skipjack tuna in Hawaii, 1952-64.

varied around an average of about 5,700 pounds per Class 2 trip. The fishing intensity exhibited a slightly declining trend from about 1953 to 1958 and leveled off at about 1,600 Class 2 trips in 1959-64.

The catch per standard effective trip and the total catch fluctuated similarly in all years except 1964. In that year, the total catch rose about 1.0 million pounds from the previous year, but the catch per standard effective trip declined 400 pounds. The catch per standard effective trip and the fishing intensity were not correlated. This result suggested that changes in the catch per standard effective trip were not influenced by changes in the amount of fishing, but by other fishery-independent factors such as variation in the availability and behavior of fish on the fishing grounds; the strength of year classes also may be important (Rothschild, 1965). The fishing intensity tended to decline over the years, largely because of a decrease in the number of vessels in the fleet.

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SER。LOGICAL EVIDENCE FOR INBREEDING OF LAHONTAN CUTTHROAT TROUT, *SALMO CLARKII HENSHAWI*, IN SUMMIT LAKE, NEVADA

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SEROLOGICAL EVIDENCE FOR INBREEDING OF LAHONTAN CUTTHROAT TROUT, *SALMO CLARKII HENSHAWI*, IN SUMMIT LAKE, NEVADA[1]

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Tests with isoimmune sera of rainbow trout, *Salmo gairdnerii*, have demonstrated blood types in Lahontan cutthroat trout. The more uniform reactivity in cutthroat trout from Summit Lake than in those from Catnip Reservoir indicated a greater degree of genetic homogeneity that may have resulted from inbreeding in the Summit Lake population. Blood typing techniques are applicable to trout breeding and management practices.

INTRODUCTION

The effects of civilization and indiscriminate stocking have drastically reduced the numbers of pure Lahontan cutthroat trout, once a major inland subspecies. Through historical research and meristic evidence, Behnke (1960) concluded that the Lahontan cutthroat trout of Heenan Lake, California (the major source for propagation in California and Nevada), although superficially a typical Lahontan fish, likely contains some rainbow trout genes. Summit Lake, Nevada, contains what Behnke considers a pure type of Lahontan cutthroat trout. The Summit Lake cutthroat population is therefore a brood stock of ichthyological and fish-cultural importance. In recent years, fry survival from matings among Summit Lake cutthroat trout has been poor; however, in outbreedings of Summit Lake fish with other cutthroat varieties, fry survival has been excellent. This difference led biologists to suspect that the Summit Lake strain might be inbred to a dangerous extent.

The work described here was an attempt to investigate, through blood-grouping techniques, the possibility of inbreeding. Research among higher vertebrates has shown that blood groups may reflect individual variations of a single locus, and that these blood groups usually are resistant to environmental influences (Race and Sanger, 1962). Similar advantages have been demonstrated in blood groups of fish where such data have been available (Cushing, 1964). Bingham (1963) presented evidence for strain-specific blood-group antigens of cutthroat trout using antisera from rainbow trout immunized with tissue preparations of cutthroat trout. Ridgway (1962a, 1962b, 1964) demonstrated the existence of numerous blood groups in rainbow trout and Pacific salmon (*Oncorhynchus* spp.) by using rainbow trout isoimmune sera. Calaprice and Cushing (1964) examined the antigenic diversity among a number of species and strains of California trouts by using a variety of normal and immune sera. They concluded that this diversity formed recognizable markers which could be used to advantage in a number of studies relating to the biology and management of California trouts. Sanders and Wright (1962) also demonstrated the existence of blood groups in several trout species, and pointed out their potential usefulness for management and biological studies.

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[1] Submitted for publication January 1966.

MATERIALS AND METHODS

Selected isoimmune sera of rainbow trout were used in this study because of their ability to detect individual variations in various salmonid species. Ridgway (1962b) presented evidence that antibody specificities of isoimmune sera of rainbow trout are under simple genetic control. We have accumulated additional evidence (unpublished) supporting these observations. Since inbreeding leads to a greater proportion of homozygous individuals in a population, a more uniform reaction may be anticipated when red blood cells from an inbred population are tested with these reagents; this uniformity reflects the genetic homogeneity of the inbred group.

Red blood cells were tested from 19 fish from Summit Lake and 20 fish from Catnip Reservoir, which had been stocked in years past with cutthroat trout from Heenan Lake. Anesthetized adult fish were bled by cardiac puncture. The cells were placed in a citrate solution and kept on ice 4 days between collection and testing. Serological tests were made by the capillary-tube agglutination method of Chown and Lewis (1946).

RESULTS

Of 40 reagents screened for reactivity with the cutthroat trout cells, 24 either did not react with any of the cells or reacted very weakly with cells from a few individuals. Six of the reagents reacted with all cells tested. The remaining 10 reagents reacted variably with cells from different trout. Of these 10 reagents, 6 were pools of numerous bleedings of individual isoimmunized rainbow trout. These reagents had been absorbed with selected rainbow trout cells so that most antibodies in a given reagent were of a single specificity. The remaining four reagents were single bleedings of isoimmunized rainbow trout which had not been absorbed, so that multiple antibody specificities may have been present (Ridgway, 1962b).

The cells from the Summit Lake cutthroat trout reacted much more uniformly with a given reagent than did the cells of fish from Catnip Reservoir. Seven of the 10 reagents reacted with cells of either all or none of the Summit Lake trout. Only 1 of 19 fish differed in qualitative reaction from the remainder with each of the other three reagents. The reactive strengths of the cells of Summit Lake cutthroat trout were also uniform. The reactive uniformity of the Catnip Reservoir trout cells, both qualitatively and quantitatively, was less for each reagent (Table 1).

The results of our research (Table 1) support the nypothesis of inbreeding in Summit Lake cutthroat trout. The high or low frequency of reaction with a given reagent indicates a high or low frequency of the gene determining the presence of the component which that reagent detects. Where reactions occur, the uniformity of reactive strengths

TABLE 1

Reactions of Red Blood Cells of 20 Cutthroat Trout from Catnip Reservoir and Summit Lake with 10 Rainbow Trout Isoimmune Reagents *

	Catnip Reservoir																					
Reagent	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Number positive	Percentage positive
260	2	1	0	0	0	2	1	0	0	2	2	1	0	0	0	0	0	0	0	0	7	35
269	2	2	0	0	2	2	0	1	1	2	0	1	1	0	0	2	1	2	0	t	13	65
297	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
304	1	1	0	0	0	2	1	0	0	2	2	1	0	0	0	0	0	0	0	0	7	35
306	0	0	1	1	1	0	t	0	1	1	0	0	0	1	0	0	0	0	0	0	7	35
316	2	2	t	2	0	2	2	t	0	1	1	1	1	t	t	0	1	0	0	0	14	70
393	0	t	1	1	1	2	1	1	0	t	t	t	1	1	1	2	0	0	t	t	16	80
412	0	1	0	2	0	2	0	1	t	2	t	t	t	0	0	t	0	0	t	t	12	60
417	t	1	0	1	0	2	0	1	t	2	0	1	1	0	t	t	1	t	1	t	15	75
507	2	3	1	2	1	2	1	2	2	2	0	2	0	2	2	2	t	1	1	1	18	90

	Summit Lake																					
Reagent	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19†	20	Number positive	Percentage positive
260	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	--	0	1	5
269	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	--	2	19	100
297	1	1	1	1	1	t	1	t	t	1	1	1	1	1	1	1	t	1	--	0	18	94
304	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	--	0	0	0
306	2	2	2	2	2	2	2	2	2	2	1	2	2	2	2	2	1	2	--	2	19	100
316	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	--	2	19	100
393	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	--	2	19	100
412	1	1	1	1	t	1	1	1	t	1	1	1	1	1	1	1	1	1	--	1	19	100
417	1	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	1	2	--	2	19	100
507	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	--	0	1	5

* Numbers in body of table indicate strength of reaction: 3—very strong; 2—strong; 1—distinct; t—weak; 0—no reaction.
† Sample hemolyzed

suggests possible homozygous conditions through the absence of detectable dosage effects. The Catnip Reservoir data reflect a mixture of genotypes with intermediate reactive frequencies and considerable quantitative fluctuations among individual fish with most reagents that produced reactions.

Chi-square tests were made between the two groups to compare the frequency of reactions of the 10 reagents used (Table 1). Seven of the tests were significant at the 1-percent level and the remaining three were significant at the 5-percent level. Reagents 297 and 507 were particularly discriminating for the two groups.

DISCUSSION

The reagents and techniques used in this work could be applied usefully to similar problems. Indications of inbreeding of brood stock could be detected and remedial measures taken before excessive losses of progeny developed. The differences in frequencies of reaction between the two groups tested may have additional implications for management. Relative survival of fry or degree of interbreeding might be estimated in areas where both Heenan Lake and Summit Lake fish have been planted.

An extension of blood-group testing for inbreeding in hatcheries could be the development of ''blood lines'' where different lots of fish are bred for particular blood-group patterns. Blood groups have proved highly valuable in identification and registration of various domestic animals (Stormont, 1958). By selecting for given blood types in breeding programs, hatcheries might identify individuals from various strains by reactive patterns of red blood cells. Selection only for antigens of red blood cells theoretically should have a minimal effect on survival. The reactions of isoimmune reagents of many of the rainbow trout with most salmonid species indicate that reagents can be produced in the more hardy species for blood-grouping work throughout the family.

This study demonstrates a further example of the rapidly expanding use of serological methods in fishery research during the past 15 years. We are continuing our research into the various specificities of the isoimmune sera of rainbow trout and their genetic interrelationships. We hope that the results presented here will lead to further application of serological methods to fishery problems.

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Clinostomum marginatum in Steelhead Trout (*Salmo gairdneri*) and Cutthroat Trout (*Salmo clarki*) in a Western Washington Lake

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ABSTRACT

Clinostomum marginatum (Trematoda : Clinostomatidae), the yellow grub parasite, was recorded in epizootic proportions from Lynch Lake, King County, Washington, in 1961 and 1962. The parasite larvae occurred principally in steelhead trout (*Salmo gairdneri*); cutthroat trout (*S. clarki*) were infected to a relatively minor degree. Fish and snail host populations were destroyed by rotenone and copper sulfate treatments.

INTRODUCTION

Heavy infections of the yellow grub parasite, *Clinostomum marginatum* (Rudolphi, 1819), occurred in steelhead trout, *Salmo gairdneri*, following their stocking as fingerlings into Lynch Lake, King County, Washington, in 1959 and 1961. Relatively light infections occurred in native cutthroat trout (*S. clarki*).

These noxious trematode larvae have been reported from at least 12 families of North American freshwater fishes, typically from warmwater species native to central and eastern drainages of the United States and southern Canada. Salmonid species have been involved only rarely (Linton, 1911; Hunter and Hunter, 1935; Haderlie, 1953; Northcote, 1957), and, where quantitative information was given, infection incidence and intensity were low.

The records of Bangham (1951), Haderlie (1953), Bangham and Adams (1954), and Northcote (1957) established the presence of *C. marginatum* in Wyoming (upper Snake River drainage), northern California, the British Columbia mainland (upper Columbia and Fraser River drainages), and Vancouver Island, respectively. This account is the first record of its occurrence in fishes from Washington. The absence of *Clinostomum* records from Oregon, and from the lower Snake River region of eastern Washington, which was surveyed by Griffith (1953), suggests that *Clinostomum* may as yet have only a spotty distribution in Pacific-slope waters.

The life history of *C. marginatum* was worked out by Hunter and Hunter (1935). Briefly, the cycle involves planorbid snails of the genus *Helisoma*, various fishes as intermediate hosts, and herons, gulls, and cormorants as definitive hosts. Readers are referred to the illustrated accounts of Lagler (1952), Davis (1953), and Meyer (1954) for specific details of the parasites' life cycle. The unsightly appearance of these parasites in food fishes is a matter of concern to anglers and fishery managers alike. Infected fish populations offer only limited reward to anglers, yet the continuance of such stocks simply perpetuates the risk of parasite dispersal to other waters containing valued fish stocks.

ENVIRONMENT AND STUDY MATERIALS

Lynch Lake is a 23-acre oligotrophic lake located in a coniferous forest basin at an elevation of 1,325 feet some 9 miles east-northeast of Carnation, Washington. It has a maximum depth of 50 feet and is fed by springs and surface runoff. The lake has no inlet, but drains by a well-defined outlet stream to the south fork of the Tolt River, an important steelhead trout habitat. The littoral zone of the lake is greatly cluttered with floating and sunken logs, submerged limbs, and slash from logging operations conducted in the lake basin prior to 1940.

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In 1958 the lake was selected by Washington State Game Department for experimental plants of steelhead trout. The objective of the program was to provide natural, competitor-free rearing conditions for hatchery-raised fingerlings. The planted fish would, after 1 or 2 years of residence, presumably migrate to sea and ultimately return to augment the native runs of steelhead in the Tolt River system.

In September (1958) the lake was closed to public fishing and a low-barrier dam was constructed at the outlet to maintain water level and to prevent entry of wild fish from the stream below. Resident fish populations were then eliminated by applying liquid and powdered rotenone at a calculated concentration of 0.5 ppm. Cutthroat trout and bridgelip suckers (*Catostomus columbianus*) were the only fish species observed, and it was assumed that the fish-kill was complete. Fish samples were not collected by the working party, so it is not known whether *Clinostomum* was present in these original residents. The initial plant of 15,000 steelhead fingerlings (344/lb.) was made in mid-May of the following spring.

Field and laboratory studies were conducted intermittently in 1961 and 1962 following discovery of *Clinostomum* larvae in fish samples taken routinely with gill nets in April and November 1960. The latter sample yielded six steelhead and two cutthroat trout, but only the steelhead were infected. We can offer only two explanations for the appearance of the cutthroat trout; they were survivors of the rotenone treatment of 1958, or the species had re-entered the lake from the outlet stream during occasional high-water spillage over the earthen abutments of the outlet structure. No other fish species appeared in the lake through late 1962 when it was rehabilitated a second time, first with rotenone (0.5 ppm) and later with copper sulfate (0.5 ppm as Cu^{++}), to rid the lake of infected fish and the resident *Helisoma* population preparatory to a new stocking effort. It is noteworthy that the second rotenone treatment, applied in early September 1962, apparently killed all remaining steelhead trout and many cutthroat trout, but follow-up gill-net checks and the ensuing copper sulfate treatment in mid-November revealed that significant numbers of cutthroat had survived the rotenone treatment. The period between the two chemical applications was one of minimum flow and minimum likelihood of cutthroat re-entry. Thus, it appears that cutthroat trout are relatively resistant to rotenone under the described conditions of exposure.

TABLE 1.—*Incidence and intensity of* Clinostomum marginatum *infections in steelhead and cutthroat trout from Lynch Lake, Washington, in 1961 and 1962*[1]

Year and species	Number examined	Mean length (inches)	Mean weight (grams)	Number infected	Mean number and range of larvae in infected fish
1961					
Steelhead	14	8.4	92.7	13	469 (27–1,036)
Cutthroat	25	7.2	63.1	4	15 (1–27)
1962					
Steelhead	20	9.3	135.8	18	68 (5–181)
Cutthroat	20	7.9	90.4	2	4 (1–6)

[1] 1962 samples taken 4 and 5 September, following rotenone application. *Clinostomum* counts from caudal portion of fish *only* (see text).

Most steelhead trout were grossly infected. Total counts of larvae in a 10-fish sample collected in May 1961 showed extensive infection of the head region, with some 40% of the overall count located in the gill tissues, inner surfaces of the operculum and branchiostegals, connective tissues of the lower jaw and tongue, and the musculature and connective tissues of the orbital region. Those occurring in the body region were extensively distributed beneath the skin, throughout the body musculature, and upon the visceral organs. Concentrations of larvae were almost invariably clustered about the basal elements of the median fins, i.e., the interneurals and interhaemals, and about the hypural complex.

Although initial samples of cutthroat trout were *Clinostomum*-free, later collections showed low rates and levels of infection. The differential infection of the two species is indicated in Table 1. Because of the tedious, time-consuming effort necessary to dissect, isolate, and count all larvae, and because relative degree of infection was the criterion of interest, the 1962 fish were not examined in their entirety. Instead, the tail portion of the fish was cut off transversely just in front of the adipose fin. The corresponding portions of each fish were proportionately equal and included the bulk of the caudal peduncle and the hypural region which, as noted earlier, was usually a site of larval concentration. The question of constant proportionality of larval distribution in the caudal section contrasted to that over the entire fish was not examined critically, but cursory examination of many other parasitized specimens suggests strongly that a significant proportion of the parasite burden regularly accumulates in that region.

The snail hosts of this parasite were surprisingly scarce despite the high levels of infection in the fish. Among 530 adult snails collected in 1961, only two harbored *Clinostomum* sporocysts. Young-of-the-year snails, presumably the major source of infection (Edney, 1950), were found only infrequently and none of those collected was infected.

Specific identity of the larval forms of the parasite was verified in a series of laboratory experiments. Metacercariae from the trout were reared to maturity using day-old cockerel chicks as experimental hosts. Egg masses of *Helisoma* were found on the undersides of spatterdock (*Nuphar* sp.) leaves as early as the 3rd week of May in 1962. These were hatched and reared in laboratory aquaria to provide a source of juvenile snails for infection experiments to determine seasonal aspects of cercarial development. A great blue heron (*Ardea herodias*) shot at the lake on 17 July yielded one gravid specimen of *C. marginatum* from the base of its tongue. The egg capsules were dissected from the uterus of this worm and apportioned equally to aquaria containing a total of 75 laboratory-reared *Helisoma* ranging from 3 to 5 weeks in age. Free-swimming cercariae first appeared on 13 October, some 3 months following introduction of the embryonated worm eggs. Two days later, seven of the surviving 65 snails were producing cercariae. These snails were placed in aquaria with laboratory-reared guppies (*Lebistes reticulatus*) which shortly exhibited the typical yellowish cysts of *Clinostomum* metacercariae.

Evidence of the longevity of metacercariae in fish was obtained from observations of a group of naturally infected steelhead and cutthroat trout that were collected by angling in early July 1962 and maintained at the laboratory in aquaria continuously supplied with dechlorinated city water. These fish died on 23 January 1964 due to a nocturnal failure of the water supply. Three steelhead and one cutthroat were dissected and yielded many vigorous larvae. Thus, natural infections persisted for almost 19 months plus whatever time the larvae resided in the fish prior to capture.

The concluding effort at Lynch Lake was to stock again with steelhead fingerlings and follow their progress. Potentially lethal levels of copper (determined through water analysis by Lauck's Testing Laboratory, Seattle, and toxicity bioassay in live-cars) persisted until July 1963, but high water temperature and a paucity of food organisms indicated by plankton samples at that time dictated a prolonged recovery period. On 18 October 1963, 10,000 steelhead fingerlings (80/lb.) were finally planted. This population was sampled by gillnetting and angling during the spring and summer of 1964 and found to be free of *Clinostomum*. Repeated search for snails produced none and it appears that complete eradication of these vectors was achieved.

DISCUSSION

The observations reported here suggest that *C. marginatum* can reach epizootic proportions in trout populations under conditions which might prevail in many lake environments. Whether cutthroat trout are, in fact, less vulnerable to infection was not demonstrated, but it is evident that steelhead, at least, are highly susceptible. If other, more commonly stocked trout species such as rainbow and brown trout (*S. trutta*) are similarly vulnerable, preventive measures may be desirable in lake rehabilitation situations where *Helisoma* is present. This suggestion, however, presupposes the development and acceptance of a molluscicide or molluscicide–piscicide superior to any chemical compound in current use.

We do not recommend the use of copper sulfate as a *routine* management practice. Although copper sulfate is an efficient molluscicide, algicide, and piscicide, there is ample evidence in the literature that its toxicity to fishes and other aquatic biota may persist for long periods after initial application. Copper sulfate was used in this instance to correct an untenable experimental situation, and then only because of its reasonably predictable effects.

The long-term effects of other molluscicidal compounds, particularly chlorinated hydrocarbons, are unsatisfactorily known at present. Much further research is needed in this area to develop management techniques that will be safe, yet effective against *Helisoma* and a variety of other molluscan hosts of other fish parasites.

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PREDICTION AND CONTROL OF STREAM TO BED INTERCHANGE IN A SALMON SPAWNING STREAM

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Intragravel water flow, i.e., the seepage of water within a streambed, is described by Darcy's law and a continuity equation where geometry and boundary conditions of the streambed are specified. The direction of exchange of water between a stream and the streambed interior (interchange) may be predicted from streambed gradient, permeability, and geometry.

Investigations with an analog computer and laboratory streambed models and observations in salmon spawning streams have shown that mathematical models have correctly predicted the direction and magnitude of intragravel water flow and interchange.

Direction of water flow may be controlled and the magnitude of interchange may be increased by manipulating stream flow or streambed permeability, permeability gradient, or streambed depth.

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EXPERIMENTAL TAGGING OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*[1]

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A practical and feasible method of tagging northern anchovies was found in a series of experiments conducted in live bait tanks in San Diego Bay. A small steel tag was inserted into the visceral cavity. An antibiotic paste of 10% tetracycline was required on the tag to prevent infection. Greater mortality occurred among fish anesthetized during tagging than among those tagged without anesthetic. Better survival occurred in freshly caught anchovies than in fish which had been held in the tanks for a few days.

INTRODUCTION

A tagging program may be needed in the near future to investigate the population structure, movement, and abundance of the northern anchovy. Studies of migration and population structure of pelagic fishes have been accomplished by tagging individual fish and by recovering them at extended time intervals (Hart and Tester, 1937; Clark and Janssen, 1945). The insertion of tags into pelagic fish is usually traumatic, and may result in a high initial mortality. Anchovies are notoriously susceptible to injury when handled, so a feasibility study was conducted to determine whether they could be tagged successfully. The experiments were designed to test the effects of several factors on fish mortality and tag loss: (i) anesthetic, (ii) tag size, (iii) handling, (iv) antibiotic, and (v) tagging conditioned and unconditioned fish.

Since the major source of tag returns in a tagging program would be from commercial canneries and reduction plants, metal tags would be required because they can be recovered by magnets or metal detectors in conveyors and reduction lines. A small nickel-plated steel internal tag (13 x 3 x 0.5 mm) with rounded ends was chosen. This type of tag has been used successfully on Pacific sardines, *Sardinops caeruleus* (Hart, 1937; Janssen and Aplin, 1945), Pacific herring, *Clupea pallasii* (Hart and Tester, 1937), and anchovetas, *Cetengraulis mysticetus* (Bayliff and Klima, 1962).

A preliminary experiment was performed to find a suitable place on the fish for tag insertion. Several anchovies were anesthetized in a solution of 7 ppm. quinaldine (2-methylquinoline, Eastman P216). A tag was inserted into the body cavity of each fish through a small incision through the lateral wall. These incisions were made by scalpel at various locations along the side and belly of the fish. All tags were inserted by pushing them anteriorly through the incision with small

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[1] Submitted for publication May 1966.

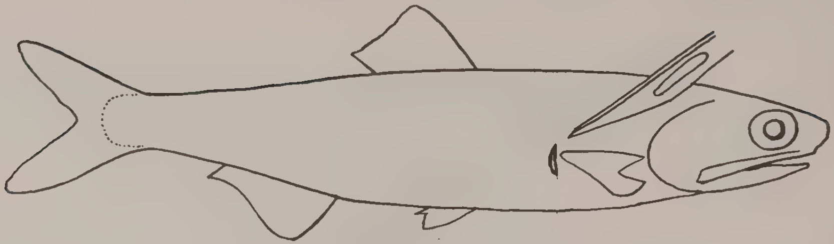

FIGURE 1. Location of incision for tag insertion.

forceps. The tagged fish were held in a small enclosure for 2 hours, killed, and dissected to determine the ultimate location of the tag and the amount of injury to internal organs. All the fish lived through this 2-hour test, although some sustained organ damage that probably would have been fatal. The most promising location for tag insertion appeared to be just dorsal to the tip of the pectoral fin (Figure 1). Fish tagged in this way showed no visible organ damage. The tags were inserted anteriorly through the incision, but the body movements of the fish moved the tags posteriorly past the point of insertion, where they lodged in a ventro-lateral position just anterior to the vent.

All anchovies used in our experiments were caught by commercial bait fishermen and placed in receivers at a live-bait barge anchored in San Diego Bay. The experiments were conducted in four, 5 x 10-foot enclosures, 5 feet deep. The sides of the enclosures were $\frac{5}{8}$-inch-mesh nylon netting, and the bottoms were plastic window screening with mesh fine enough to retain any tags the anchovies might lose. Shed tags were collected daily by sweeping the bottom of the enclosure with a magnet.

EXPERIMENTS

Experiment I: Anesthesia but no Control of Infection

In the first experiment (I), 200 anchovies were anesthetized, tagged, and released into one of the enclosures; 200 others were placed in an adjoining enclosure as controls. The control fish were handled in exactly the same manner as the tagged fish, including anesthetization and making an incision through the body wall, but no tags were inserted. This procedure was intended to distinguish the mortality caused by handling from that directly attributable to the tags. One hour after the tagging was completed, all dead fish were removed. This immediate mortality was deducted from the original number tagged and the remaining fish were considered successfully tagged. Because the immediate mortality varied considerably among experiments, all the calculations reported in this paper are based on percentages of the successfully tagged fish or living controls.

During the first five days, 18.3% of the controls and 31.6% of the tagged fish died. The mortality of tagged fish increased on the sixth day and continued at a high rate, but mortality among the controls decreased (Table 1, Figure 2). The high mortality of tagged fish after the sixth day appeared to be caused by a heavy bacterial infection; the internal organs were inflamed and edemic. No effort had been made to maintain sterile conditions during tagging. The experiment was terminated after 11 days, when 80.2% of the tagged fish and 19.3% of the control fish had died.

TABLE 1

Experiment Number I—Mortality in 200 Tagged Anchovies and 200 Control Fish

Days after tagging	Mortality of tagged fish		Mortality of control fish	
	Number	Percentage*	Number	Percentage*
0†	13		8	
1	15	8.0	5	2.6
2	15	8.0	13	6.8
3	14	7.5	4	2.1
4	5	2.7	8	4.2
5	10	5.4	5	2.6
6	20	10.7	1	0.5
7	18	9.6	0	0
8	24	12.8	1	0.5
9	17	9.1	0	0
10	9	4.8	0	0
11	3	1.6	0	0
Totals	**150**	**80.2**	**37**	**19.3**

* The values are percentages of tagged or control fish alive after 1 hour.
† Immediate mortality, fish dead within 1 hour after completion of tagging (not included in totals).

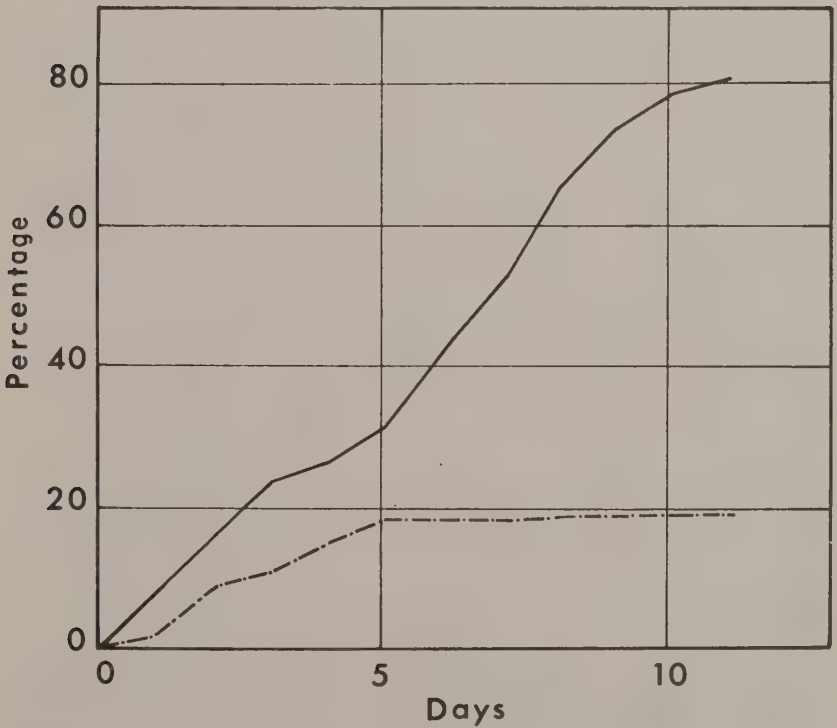

FIGURE 2. Experiment I. Cumulative percentage mortality among anchovies tagged with regular-size tags (solid line) and control fish (broken line). The data are from Table 1.

Experiment II: Control of Infection Attempted; Tag Size Tested

The second experiment (IIa, b, c), designed to test methods of preventing the bacterial infection observed in experiment I, and to determine if tag size had any effect on survival, consisted of three separate tests and a control. All the tags and instruments were soaked in 90% alcohol to reduce bacterial contamination. The tags were air dried on a sterile surface before insertion. Scalpel blades and forceps were wiped with alcohol after each fish was handled.

In experiment IIa, 200 anchovies were tagged with sterilized regular-size tags (13 x 3 x 0.5 mm) without antibiotic. In experiment IIb, 200 fish were tagged with the same size tags coated with an antibiotic paste of 10% tetracycline HCl in sterile petrolatum. Tetracycline was chosen because it is a broad-spectrum antibiotic with an apparently low toxicity to fish. It has a secondary advantage of making a mark on otoliths and bones after it is administered (Kobayashi, 1964); this could provide additional information on age and growth. The paste form was used because it could be applied with the tag in a single operation, thus eliminating the additional time and handling of fish required for injection of the antibiotic.

In experiment IIc, 200 anchovies were marked with tags approximately half the size of the regular tags (6 x 3 x 0.5 mm), without antibiotic. Again 200 anchovies were used for controls and were handled exactly like the controls in experiment I.

Immediate mortality (fish dead within one hour after tagging) was 47 in the control, 54 in IIa, and 66 in IIc. These losses, which were considerably higher than those in experiment I, appeared to be caused by over-anesthesia. In test IIb, the length of time the fish were anesthetized was shortened by putting fewer fish at a time in the anesthetic; the immediate mortality was only 16 fish in this group.

Maintenance of sterile conditions during tagging appeared to be advantageous. The increase in infection-induced mortality after the sixth day was again noted in the fish tagged with the regular-size tag without antibiotic (experiment IIa, Table 2, Figure 3), but the rate of loss was only about half that of experiment I. Total mortality after 26 days amounted to 61.6% of the successfully tagged fish. The antibiotic on the regular-size tag in experiment IIb reduced the mortality even further, to 21.2%, but the lowest mortality was observed in IIc —fish tagged with the small tag without antibiotic. In IIc the total loss was only 3.7% after 26 days. The smaller tag probably lessened mortality by reducing mechanical injury and infectious material.

Each day all dead fish were dissected and examined, tag locations were noted, and visible internal damage was recorded. Three fish from experiment IIa and two from IIb died after thay had shed their tags. These fish were not included in the daily mortality because they had already been accounted for in the tags-shed and mortality-plus-tags-shed columns (Table 2).

Tag shedding, which did not occur during the short duration of experiment I, was important in experiment II. More regular-size tags with antibiotic were shed (22.3%) than regular tags without antibiotic (11.6%). Two factors were involved: the antibiotic tended to inhibit healing of the incision, and the high mortality of fish in IIa probably accounted for some fish that would have shed tags later. The small

TABLE 2

Experiment Number II—Mortality and Tag Loss in 600 Tagged Anchovies (200 in Each Experimental Lot) and 200 Control Fish

Days after tagging	Experiment IIa Regular tags (13 x 3 x 0.5 mm) without antibiotic						Experiment IIb Regular tags (13 x 3 x 0.5 mm) with antibiotic						Experiment IIc Small tags (6 x 3 x 0.5 mm) without antibiotic						Control	
	Mortality		Tags shed		Mortality plus tags shed		Mortality		Tags shed		Mortality plus tags shed		Mortality		Tags shed		Mortality plus tags shed		Mortality	
	No.	%*	No.	%*	No.	%*	No.	%*	No.	%*	No.	%*	No.	%*	No.	%*	No.	%*	No.	%*
†0	54		0		54		16		0		16		66		0		66		47	
1	4	2.7	3	2.0	7	4.8	3	1.6	8	4.5	11	6.0	3	2.2	6	4.5	9	6.7	2	1.3
2	11	7.5	0	0	11	7.5	2	1.1	0	0	2	1.1	0	0	0	0	0	0	3	2.0
3	0	0	0	0	0	0	1	0.5	7	3.8	8	4.3	0	0	1	0.8	1	0.8	0	0
4	1	0.7	0	0	1	0.7	3	1.6	1	0.5	4	2.2	0	0	2	1.5	2	1.5	1	0.6
5	4	2.7	1	0.7	5	3.4	3	1.6	2	1.1	5	2.7	1	0.8	3	2.2	4	3.0	0	0
6	4	2.7	0	0	4	2.7	0	0	0	0	0	0	0	0	1	0.8	1	0.8	0	0
7	18	12.3	0	0	18	12.3	3	1.6	2	1.1	5	2.7	1	0.8	2	1.5	3	2.2	0	0
8	9	6.2	0	0	9	6.2	2	1.1	0	0	2	1.1	0	0	1	0.8	1	0.8	0	0
9	7	4.8	1	0.7	8	5.5	6	3.3	1	0.5	7	3.8	0	0	2	1.5	2	1.5	0	0
10	5	3.4	0	0	5	3.4	5	2.7	0	0	5	2.7	0	0	1	0.8	1	0.8	1	0.6
11	3	2.0	1	0.7	4	2.7	1	0.5	3	1.6	4	2.2	0	0	2	1.5	2	1.5	0	0
12	3	2.0	2	1.4	5	3.4	1	0.5	2	1.1	3	1.6	0	0	4	3.0	4	3.0	0	0
13	2	1.4	2	1.4	4	2.7	0	0	3	1.6	3	1.6	0	0	1	0.8	1	0.8	0	0
14	0	0	0	0	0	0	0	0	2	1.1	2	1.1	0	0	5	3.7	5	3.7	0	0
15	1	0.7	1	0.7	2	1.4	1	0.5	1	0.5	2	1.1	0	0	0	0	0	0	0	0
16	1	0.7	0	0	1	0.7	1	0.5	2	1.1	3	1.6	0	0	4	3.0	4	3.0	0	0
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	1	0.7	1	0.7	2	1.4	0	0	2	1.1	2	1.1	0	0	2	1.5	2	1.5	1	0.6
19	0	0	1	0.7	1	0.7	0	0	2	1.1	2	1.1	0	0	0	0	0	0	0	0
20	0	0	2	1.4	2	1.4	2	1.1	0	0	2	1.1	0	0	3	2.2	3	2.2	0	0
21	1	0.7	0	0	1	0.7	0	0	1	0.5	1	0.5	0	0	3	2.2	3	2.2	0	0
22	1	0.7	2	1.4	3	2.0	0	0	0	0	0	0	0	0	2	1.5	2	1.5	0	0
23	3	2.0	0	0	3	2.0	1	0.5	1	0.5	2	1.1	0	0	0	0	0	0	2	1.3
24	4	2.7	0	0	4	2.7	1	0.5	1	0.5	2	1.1	0	0	1	0.8	1	0.8	0	0
25	2	1.4	0	0	2	1.4	1	0.5	0	0	1	0.5	0	0	1	0.8	1	0.8	0	0
26	2	1.4	0	0	2	1.4	0	0	0	0	0	0	0	0	1	0.8	1	0.8	0	0
Totals	87	59.6	17‡	11.6	104	71.2	37	20.1	41‡	22.3	78	42.4	5	3.7	48	35.8	53	39.6	10	6.5

* The values are percentages of tagged or control fish alive after one hour.

† Immediate mortality, fish dead within one hour after completion of tagging (not included in totals).

‡ Three fish from experiment IIa that had shed tags and two from IIb subsequently died. They were not included in the mortality column because they had already been accounted for in the mortality-plus-tags-shed column.

tags were shed more rapidly (35.8%) than the regular-size tags with or without antibiotic, presumably because the shorter length of the small tag allowed it to orient more readily to the position of the wound.

Experiment III: Method of Inserting Tag; Tagging Without Anesthetic

Experiment III was designed to see if the amount of shedding (22.3% in IIb and 35.8% in IIc) could be cut down by inserting tags through the incision posteriorly rather than anteriorly, and to test the effect of tagging without anesthetic.

Tags inserted anteriorly were usually moved caudad by the body movements of the fish. It was postulated that if the tags were inserted posteriad originally they would have less chance to move past the open wound and be shed. Experiment III consisted of three separate tests in which all the tags were inserted posteriorly. In experiment IIIa, 200 anchovies were tagged with the regular-size tags without antibiotic; in IIIb, 200 fish were tagged with the regular-size tags with tetracycline antibiotic; in IIIc, 200 fish were tagged with the small tag without antibiotic; and 200 anchovies served as controls. No anesthetic was used in any of the tests or the control. Immediate mortality accounted for only 1 of the 200 control fish and none of the 600 tagged anchovies.

In experiment IIIa, the mortality was very high (91.0%), and appeared to be caused by extremely heavy infection, even though the sterile conditions of the previous experiments were maintained (Table 3, Figure 4). We believe that the infection was fostered by the warmer water, which averaged 67.2° F, compared with 63.9° F during experiment II. The effectiveness of the antibiotic can be seen readily in experiment IIIb, which differed from IIIa only in the use of the tetracycline paste. The mortality in IIIb (28.0%) was much less than in IIIa (91.0%). In experiment IIIc (fish tagged with the small tags without antibiotic) mortality also increased to 30.0%, compared with 3.7% in the previous experiment.

During the last six days of experiment III, water in San Diego Bay was extremely dirty and a heavy oil slick appeared around the bait receivers. These water conditions may have contributed to the increased mortality during that period.

Insertion of tags in a posterior direction reduced the amount of shedding among fish that were tagged with the regular-size tags from 11.6% in IIa and 22.3% in IIb, to 2.5% in IIIa and 12.5% in IIIb, but increased the shedding of the small tags to 58.5% in IIIc from 35.8% in IIc. When the tags were inserted anteriorly, one or two scales were removed and the incision was slanted in the direction of the scale pocket. To insert the tags in a posterior direction, more scales usually had to be removed and the incision was made at about a right angle to the body. Insertion of the tag was more difficult, and often caused a slightly larger wound, which in turn probably facilitated loss of the small tags but not the larger ones. Three of the fish tagged with the small tags (IIIc) died after they had shed their tags; they were not included in the daily mortality because they had already been accounted for in the tags-shed and mortality-plus-tags-shed columns (Table 3).

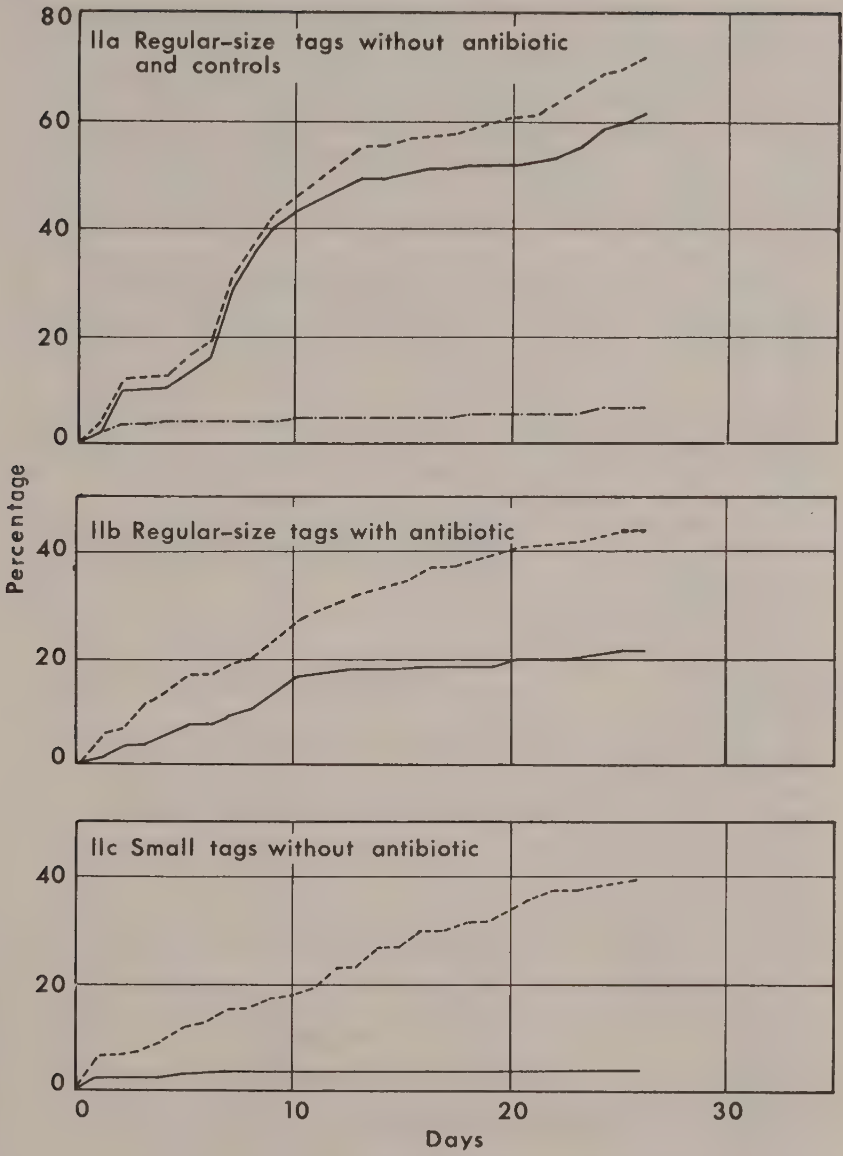

FIGURE 3. Experiment II. Cumulative percentage mortality and tag loss in tagged anchovies and control fish under different experimental conditions. Solid line shows cumulative mortality; dashed line, cumulative mortality plus shed tags; dot and dash line in Figure IIa shows cumulative mortality of controls. Graphs based on data from Table 2.

TABLE 3

Experiment Number III—Mortality and Tag Loss in 600 Anchovies (200 in Each Experimental Lot) and 200 Control Fish

Days after tagging	Experiment IIIa Regular tags (13 x 3 x 0.5 mm) without antibiotic						Experiment IIIb Regular tags (13 x 3 x 0.5 mm) with antibiotic						Experiment IIIc Small tags (6 x 3 x 0.5 mm) without antibiotic						Control	
	Mortality		Tags shed		Mortality plus tags shed		Mortality		Tags shed		Mortality plus tags shed		Mortality		Tags shed		Mortality plus tags shed		Mortality	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%*
†0	0		0		0		0		0		0		0		0		0		1	
1	1	0.5	0	0	1	0.5	0	0	0	0	0	0	2	1.0	0	0	2	1.0	1	0.5
2	4	2.0	1	0.5	5	2.5	3	1.5	1	0.5	4	2.0	11	5.5	0	0	11	5.5	0	0
3	5	2.5	0	0	5	2.5	1	0.5	0	0	1	0.5	8	4.0	0	0	8	4.0	1	0.5
4	14	7.0	0	0	14	7.0	0	0	0	0	0	0	3	1.5	0	0	3	1.5	0	0
5	23	11.5	0	0	23	11.5	1	0.5	0	0	1	0.5	3	1.5	0	0	3	1.5	0	0
6	34	17.0	0	0	34	17.0	1	0.5	0	0	1	0.5	0	0	1	0.5	1	0.5	0	0
7	34	17.0	0	0	34	17.0	5	2.5	0	0	5	2.5	0	0	0	0	0	0	0	0
8	24	12.0	0	0	24	12.0	4	2.0	0	0	4	2.0	0	0	7	3.5	7	3.5	0	0
9	13	6.5	0	0	13	6.5	5	2.5	0	0	5	2.5	0	0	10	5.0	10	5.0	0	0
10	11	5.5	0	0	11	5.5	2	1.0	1	0.5	3	1.5	0	0	11	5.5	11	5.5	1	0.5
11	4	2.0	0	0	4	2.0	2	1.0	0	0	2	1.0	0	0	12	6.0	12	6.0	1	0.5
12	3	1.5	0	0	3	1.5	0	0	1	0.5	1	0.5	0	0	9	4.5	9	4.5	1	0.5
13	2	1.0	0	0	2	1.0	2	1.0	1	0.5	3	1.5	2	1.0	13	6.5	15	7.5	0	0
14	1	0.5	1	0.5	2	1.0	0	0	2	1.0	2	1.0	2	1.0	3	1.5	5	2.5	0	0
15	1	0.5	0	0	1	0.5	3	1.5	1	0.5	4	2.0	0	0	9	4.5	9	4.5	2	1.0
16	0	0	0	0	0	0	0	0	5	2.5	5	2.5	1	0.5	7	3.5	8	4.0	0	0
17	1	0.5	0	0	1	0.5	0	0	2	1.0	2	1.0	0	0	4	2.0	4	2.0	1	0.5
18	1	0.5	0	0	1	0.5	1	0.5	2	1.0	3	1.5	1	0.5	1	0.5	2	1.0	2	1.0
19	0	0	0	0	0	0	3	1.5	1	0.5	4	2.0	0	0	8	4.0	8	4.0	0	0
20	0	0	2	1.0	2	1.0	4	2.0	0	0	4	2.0	0	0	4	2.0	4	2.0	0	0
21	1	0.5	0	0	1	0.5	2	1.0	1	0.5	3	1.5	0	0	3	1.5	3	1.5	2	1.0
22	1	0.5	0	0	1	0.5	3	1.5	1	0.5	4	2.0	0	0	2	1.0	2	1.0	2	1.0
23	1	0.5	0	0	1	0.5	0	0	1	0.5	1	0.5	1	0.5	2	1.0	3	1.5	2	1.0
24	0	0	0	0	0	0	2	1.0	2	1.0	4	2.0	1	0.5	2	1.0	3	1.5	0	0
25	0	0	0	0	0	0	2	1.0	0	0	2	1.0	0	0	0	0	0	0	3	1.5
26	0	0	0	0	0	0	0	0	0	0	0	0	1	0.5	1	0.5	2	1.0	2	1.0
27	0	0	0	0	0	0	1	0.5	1	0.5	2	1.0	2	1.0	3	1.5	5	2.5	1	0.5
28	1	0.5	0	0	1	0.5	4	2.0	0	0	4	2.0	0	0	3	1.5	3	1.5	0	0
29	1	0.5	0	0	1	0.5	1	0.5	1	0.5	2	1.0	0	0	1	0.5	1	0.5	0	0
30	1	0.5	0	0	1	0.5	1	0.5	0	0	1	0.5	0	0	1	0.5	1	0.5	2	1.0
31	0	0	0	0	0	0	0	0	0	0	0	0	6	3.0	0	0	6	3.0	2	1.0
32	0	0	0	0	0	0	0	0	0	0	0	0	6	3.0	0	0	6	3.0	3	1.5
33	0	0	0	0	0	0	0	0	1	0.5	1	0.5	6	3.0	0	0	6	3.0	3	1.5
34.	0	0	1	0.5	1	0.5	3	1.5	0	0	3	1.5	4	2.0	0	0	4	2.0	2	1.0
Totals	**182**	**91.0**	**5**	**2.5**	**187**	**93.5**	**56**	**28.0**	**25**	**12.5**	**81**	**40.5**	**60**	**30.0**	**117‡**	**58.5**	**177**	**88.5**	**34**	**17.0**

* The values are percentages of control fish alive after one hour.

† Immediate mortality, fish dead within one hour after completion of tagging (not included in totals).

‡ Three of these fish that had shed tags subsequently died. They were not included in the mortality column because they had already been accounted for in the mortality-plus-tags-shed column.

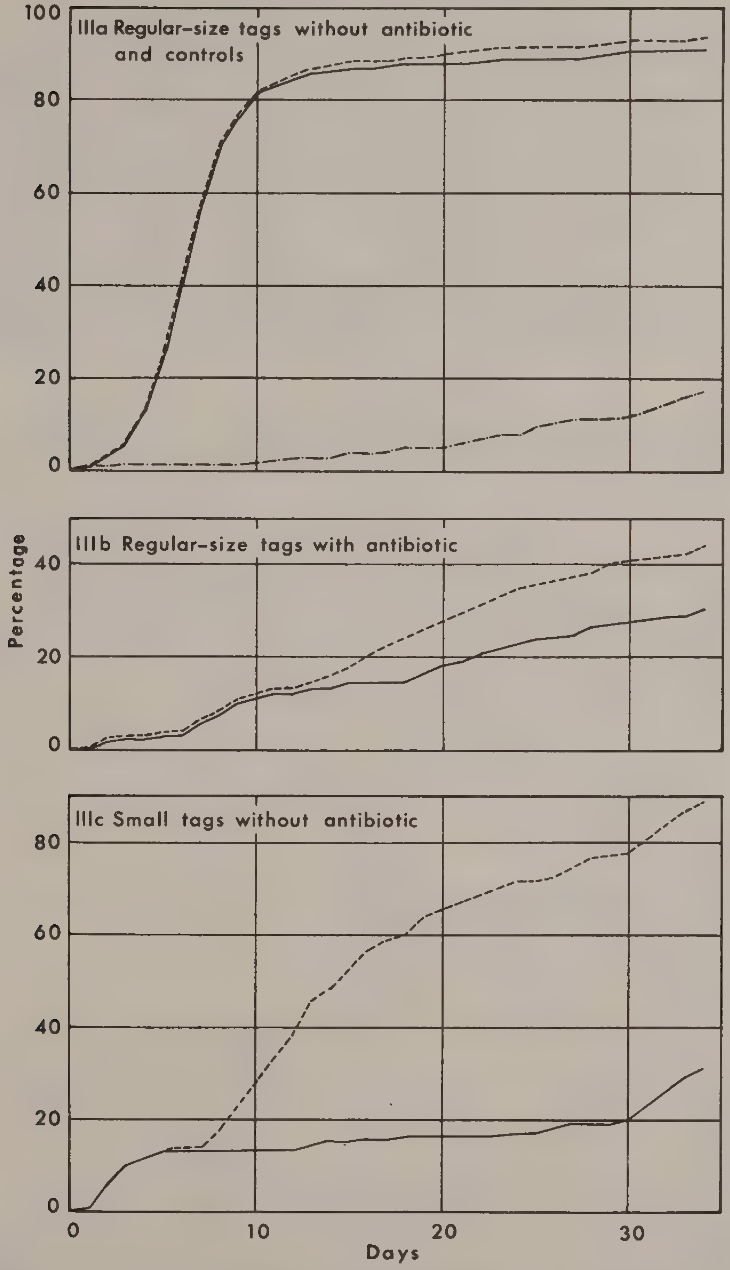

FIGURE 4. Experiment III. Cumulative percentage mortality and tag loss in tagged anchovies and control fish under different experimental conditions. Solid line shows cumulative mortality; dashed line, cumulative mortality plus shed tags; dot and dash line in Figure IIIa shows cumulative mortality of controls. Graphs based on data from Table 3.

Experiment IV: Non-conditioned Fish

All of the anchovies used in the first three experiments had been ''conditioned'' by holding them in a live bait receiver for a few days before tagging. To determine if conditioning was necessary or even useful, experiment IVa was set up with 200 freshly caught anchovies. They were tagged with the regular-size tags with tetracycline antibiotic paste, without the use of an anesthetic. The control consisted of 200 freshly caught fish. After 35 days only 10.5% of the tagged fish and 8.5% of the controls had died (Table 4, Figure 5). This is a much lower mortality than that observed in the similarly tagged conditioned fish of experiments IIb (22.3%) and IIIb (12.5%). The amount of tag shedding (9.5%) was also low. Only 20% of the fish were lost through both tag shedding and mortality at the end of 35 days.

TABLE 4

Experiment Number IV—Mortality and Tag Loss in 200 Tagged Unconditioned Anchovies and 200 Control Fish

Days after tagging	Experiment IVa Regular tags (13 × 3 × 0.5 mm) with antibiotic						Control	
	Mortality		Tags shed		Mortality plus tags shed		Mortality	
	Number	Percent	Number	Percent	Number	Percent	Number	Percent
0	0		0		0		0	
1	0	0	1	0.5	1	0.5	4	2.0
2	1	0.5	0	0	1	0.5	2	1.0
3	5	2.5	0	0	5	2.5	4	2.0
4	1	0.5	0	0	1	0.5	3	1.5
5	3	1.5	0	0	3	1.5	0	0
6	1	0.5	0	0	1	0.5	1	0.5
7	1	0.5	0	0	1	0.5	0	0
8	1	0.5	0	0	1	0.5	0	0
9	0	0	1	0.5	1	0.5	0	0
10	1	0.5	0	0	1	0.5	0	0
11	0	0	0	0	0	0	0	0
12	0	0	1	0.5	1	0.5	0	0
13	0	0	1	0.5	1	0.5	0	0
14	0	0	0	0	0	0	0	0
15	1	0.5	0	0	1	0.5	0	0
16	1	0.5	1	0.5	2	1.0	0	0
17	0	0	2	1.0	2	1.0	0	0
18	1	0.5	1	0.5	2	1.0	0	0
19	0	0	1	0.5	1	0.5	0	0
20	1	0.5	1	0.5	2	1.0	0	0
21	0	0	0	0	0	0	0	0
22	0	0	1	0.5	1	0.5	0	0
23	0	0	0	0	0	0	0	0
24	1	0.5	0	0	1	0.5	1	0.5
25	0	0	1	0.5	1	0.5	0	0
26	0	0	1	0.5	1	0.5	1	0.5
27	1	0.5	0	0	1	0.5	0	0
28	0	0	1	0.5	1	0.5	0	0
29	0	0	1	0.5	1	0.5	0	0
30	0	0	1	0.5	1	0.5	0	0
31	0	0	1	0.5	1	0.5	1	0.5
32	0	0	1	0.5	1	0.5	0	0
33	0	0	0	0	0	0	0	0
34	1	0.5	2	1.0	3	1.5	0	0
35	0	0	0	0	0	0	0	0
Totals	**21**	**10.5**	**20**	**10.0**	**41**	**20.5**	**17**	**8.5**

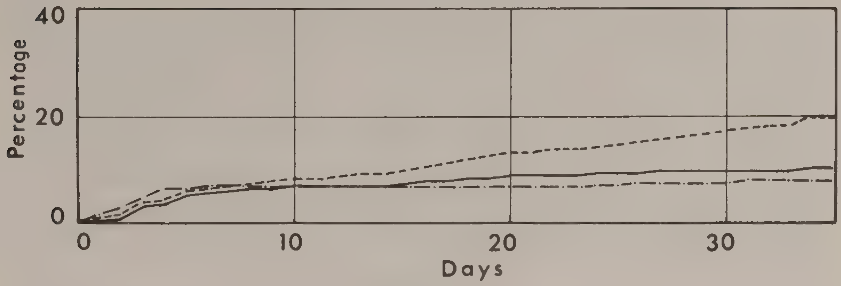

FIGURE 5. Experiment IV. Cumulative percentage mortality and tag loss in tagged unconditioned anchovies and control fish. Solid line shows cumulative mortality; dashed line, cumulative mortality plus shed tags; dot and dash line shows cumulative mortality of controls. The data are from Table 4.

Again it was demonstrated that the anesthetic was not needed. Neither the tagged group nor the control suffered any immediate mortality. Immediate mortality accounted for 204 of the 1,200 fish which had been anesthetized, but only 1 of the 1,200 handled without anesthetic (Table 5).

It would have been desirable to continue some of the experiments over a longer period, but the lack of holding space in the receivers necessitated restriction of each group of tests to about one month. If an actual anchovy tagging program is started, it would be desirable to make some longer-term experiments on a larger scale to determine more precisely the total loss of tagged fish (actual mortality plus shed tags) before tagging data are used in calculating population numbers. It is possible, however, to speculate on the tag-shedding aspect of long-term experiments. Most of the shedding had probably occurred by the end of 30 days. All the fish alive at the end of the experiments were dissected, and the tags were removed. In most, the wounds were com-

TABLE 5

Immediate Mortality (Fish Dead Within One Hour After Tagging) in Tagged and Control Anchovies, Handled With and Without Anesthetic

Experiment number	Number of anchovies used	Immediate mortality	Successfully tagged or control fish
Anesthetic used			
I	200	13	187
I Control	200	8	192
IIa	200	54	146
IIb	200	16	184
IIc	200	66	134
II Control	200	47	153
Anesthetic not used			
IIIa	200	0	200
IIIb	200	0	200
IIIc	200	0	200
III Control	200	1	199
IVa	200	0	200
IV Control	200	0	200

pletely healed and covered with new scales; in a few, the tip of the tag protruded outside the fish. Generally, the fish showed little ill effect from the tags which were encysted along the body wall, the gonads, the intestines, or the mesentery. Occasionally a tag was imbedded in the intestines, gonad, or liver, and the general condition of the fish appeared poor. Janssen and Aplin (1945), who used a similar tag on sardines, observed that the amount of shedding decreased rapidly after 20 to 25 days. Bayliff and Klima (1962) stated that most of the shedding of internal tags by anchovetas took place within the first month after tagging.

CONCLUSION

Tagging of northern anchovies with metal internal tags is feasible. The best results were obtained by using 13 x 3 x 0.5-mm nickel-plated steel tags coated with tetracycline paste and inserted posteriorly through an incision cut just dorsal to the tip of the pectoral fin. Freshly caught anchovies may be tagged without the use of an anesthetic.

SUMMARY

1) A total of 1,600 northern anchovies was tagged with metal internal tags; an additional 800 served as controls.
2) Maintenance of sterile conditions during tagging reduced the mortality over that from tagging under non-sterile conditions.
3) The mortality was less in anchovies marked with tags approximately half the size of the regular tags, but increased shedding of the smaller tags offset this advantage.
4) Mortality was reduced greatly by use of an antibiotic paste on the regular-size tags, but shedding was increased slightly. Insertion of the tags in a posterior instead of an anterior direction somewhat reduced shedding.
5) Freshly caught anchovies survived tagging better than ''conditioned'' fish.
6) Immediate mortality accounted for 204 of the 1,200 fish which had been anesthetized but only 1 of the 1,200 handled without an anesthetic.

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THE EUROPEAN OYSTER, OSTREA EDULIS, IN MAINE

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ABSTRACT

Favorable temperature and salinity characteristics of the Maine coast encouraged several introductions of Ostrea edulis from Holland. The most successful transplant was in Boothbay Harbor and surveys indicated that oysters have set annually on suitable bottom below low tide level, in and near this area, persistently increasing in abundance and range. Spat set also in the intertidal zone, but most did not survive the winters. Using shell bags on bottom, and raft-suspended shell strings, initial set was found to be greatest in shell bags, but survival through winter was greater on suspended shell strings. Not all transplants were successful, and recruitment rate is low, but the persistent expansion of the oyster population in Boothbay Harbor is encouraging.

INTRODUCTION

The decline of soft-shell clam stocks in northern New England from 1946 to 1959 emphasized the economic need for an additional fishery in intertidal or shallow subtidal environments. The successful introduction of the European oyster, Ostrea edulis L., into northern New England appeared theoretically possible. Although the coastal waters are often too cold to allow spawning, the temperature and salinity characteristics of many inshore areas are superficially similar to those in parts of the natural European habitat. According to Korringa (1940) this species thrives in the Oosterschelde of Holland, with salinity varying from 25.1 to 32.9 o/oo; also, spawning can occur at temperatures of 15 to 16 C with more successful spatfall resulting from more prolonged higher temperatures. Detailed information on temperature and salinity was not available prior to introduction of the species, but data for 1959 will serve as an example of conditions occurring in Boothbay Harbor. Daily salinity readings at the Bureau of Commercial Fisheries Biological Laboratory varied from 16.7 to 34.2 o/oo, but monthly averages of daily readings varied only from 29.0 to 32.8 o/oo. Salinities below 22.5 o/oo, a minimum for normal growth and setting of Ostrea edulis larvae (Davis and Ansell, 1962), were recorded on only three separate days. All variations were well above the 15.0 o/oo minimum found by Chanley (1958) to be suitable for Ostrea edulis juveniles. Boothbay Harbor water temperatures during the spawning season of 1959 rose well above the 15 C minimum for spawning of this oyster.

The first European oysters were introduced in 1949 and Loosanoff (1951, 1955, 1962) reported on their initial survival, gametogenesis, and spawning. There has never been a coordinated study made of the first and subsequent introductions, but this report brings together all known additional information on the existence of the European oyster in Maine. Since there has been little effort made to improve oyster setting or growing conditions in Maine, the natural increase and spread of this introduced species is of considerable ecological interest. The data have been obtained principally through observations of personnel of the Bureau of Commercial Fisheries Biological Laboratory at Boothbay Harbor, Maine, and the Maine Department of Sea and Shore Fisheries. Age or year class was determined by a combination of relative size and counts of annual rings. Unless otherwise indicated, all references to oysters in this paper are to the European species, Ostrea edulis.

TRANSPLANTATION OF OYSTERS

Over a period of 12 years, several attempts were made to introduce oysters from Holland into Maine waters. These attempts and other related transplants were as follows, with locations shown in Figs. 1 and 2.

Group 1, Basin Cove, Harpswell

This group and the two following made up the original introduction in October 1949 (Loosanoff, 1951, 1955, 1962). The oysters had been shipped from the Oosterschelde in Holland to the U. S. Fish and Wildlife Service Biological Laboratory in Milford, Connecticut, and had been carefully screened for diseases, parasites, and other potentially dangerous organisms. The lot included representatives of the 1947, 1948, and 1949 year classes and was distributed in Maine to determine survival and ability to mature sexually and spawn. In Basin Cove, 1,060 were held in cages.

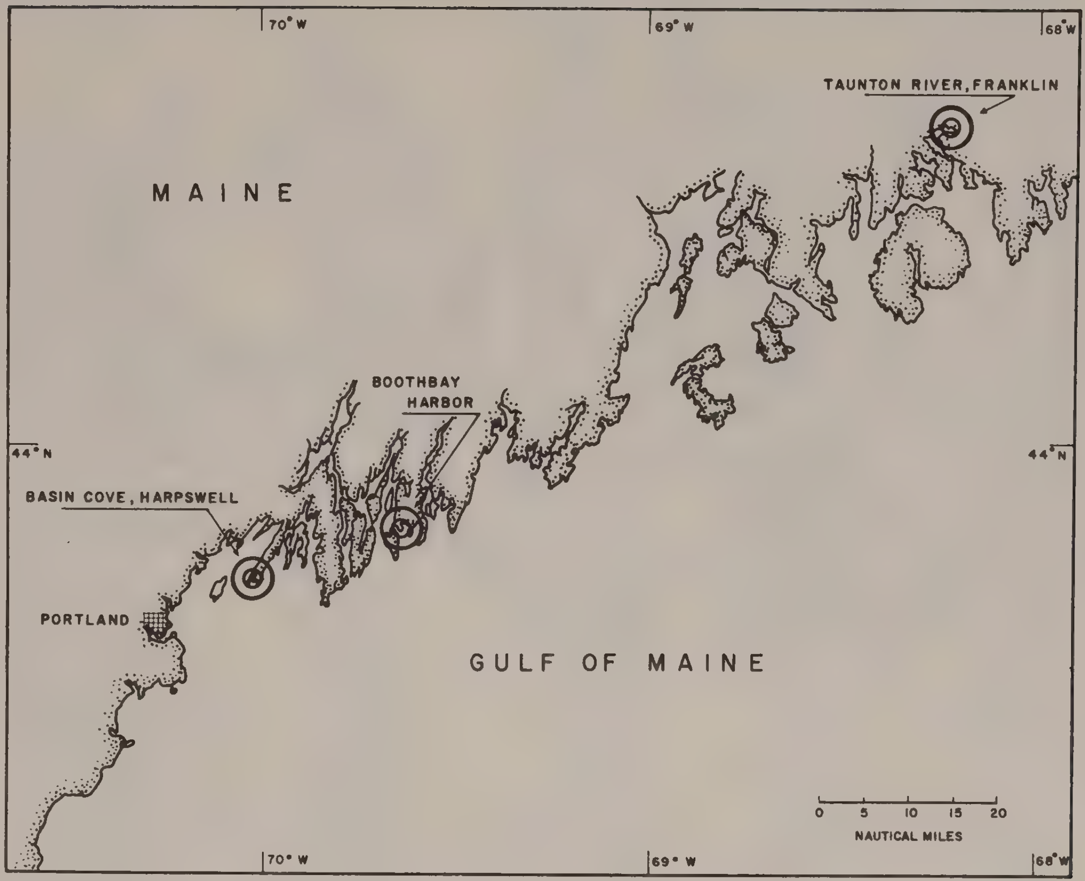
70° W
69° W
68° W
TAUNTON RIVER, FRANKLIN
MAINE
BOOTHBAY HARBOR
44° N
BASIN COVE, HARPSWELL
PORTLAND
GULF OF MAINE
0 5 10 15 20
NAUTICAL MILES

Fig. 1. Locations of the original introductions of European oysters in Maine, 1949.

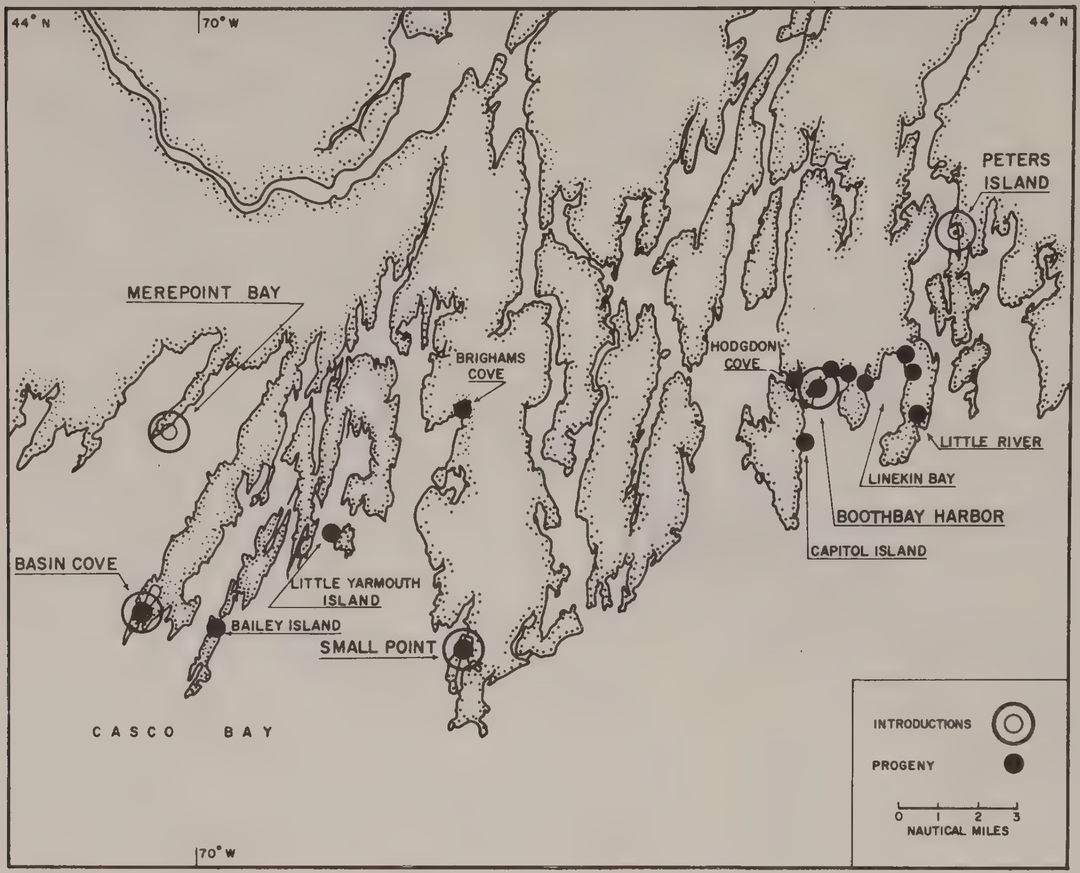
44° N
70° W
44° N
MEREPOINT BAY
PETERS ISLAND
BRIGHAMS COVE
HODGDON COVE
LITTLE RIVER
LINEKIN BAY
BOOTHBAY HARBOR
CAPITOL ISLAND
BASIN COVE
LITTLE YARMOUTH ISLAND
BAILEY ISLAND
SMALL POINT
CASCO BAY
INTRODUCTIONS
PROGENY
0 1 2 3
NAUTICAL MILES
70° W

Fig. 2. Locations of introductions of European oysters and known locations of progeny, 1949-1962.

Group 2, Boothbay Harbor

Part of the same lot as Group 1; 3,600 were held in cages.

Group 3, Taunton River, Franklin

Part of the same lot as Groups 1 and 2; 1,060 were held in cages.

Group 4, Boothbay Harbor

In June 1954, the Maine Department of Sea and Shore Fisheries imported 390 lbs of adult oysters from Holland. They were held at the laboratory wharf in an effort to augment the local spawning population of oysters (progeny of the original introductions).

Group 5, Small Point, Phippsburg

In December 1955, an estimated 4,000 Dutch oysters were privately imported in cooperation with the Maine Department of Sea and Shore Fisheries. These oysters were placed in a lobster pound as the nucleus of a spawning population.

Group 6, Peters Island, Bristol

In April 1959, personnel of the Maine Department of Sea and Shore Fisheries transferred 50 adult Boothbay Harbor oysters (progeny of the original introductions) to Peters Island to test the possibility of extending the local range more rapidly by dispersing groups of mature oysters.

Group 7, Merepoint Bay, Harpswell

In May 1961, approximately 2 bushels of oysters of various sizes from the Milford laboratory were placed in cages in shallow water. These oysters had been propagated at the Milford laboratory from Dutch stock and were placed in Merepoint Bay to serve as spawning stock.

FATES OF TRANSPLANTED OYSTERS

Group 1, Basin Cove, Harpswell

A large proportion of the oysters survived and spawned during the first 2 years when they were under close observation. By July 1954, there were 120 of the original stock alive in the cages; and in July 1962 SCUBA divers reported 55 in the immediate area of the original cages. Seven of these, examined at the laboratory, appeared to be very old and are believed to be of the original stock.

Group 2, Boothbay Harbor

A large proportion of this group survived, spawned, and produced set during its first 2 years. In May 1952, all survivors of the group, except 15 retained in laboratory tanks, were returned to the Milford laboratory. The remaining 15 were also returned in May 1953.

Group 3, Taunton River, Franklin

This group suffered heavy mortality and by November 1953 no live oysters could be found.

Group 4, Boothbay Harbor

These oysters spawned as expected during their first summer, but during the following winter and spring all were lost because of damage to the holding cages.

Group 5, Small Point, Phippsburg

Few observations were made on this group and the oysters were reported as all dead or missing the following spring.

Group 6, Peters Island, Bristol

No observations were made on this group until August 1961, when only dead shells were found.

Group 7, Merepoint Bay, Harpswell

This group was examined occasionally and dead oysters were removed. Although there was no initial count, there did not appear to be a very heavy mortality. In October 1962, 1,181 remained alive. These were removed from the cages and scattered on hard bottom about 3 feet below mean low water.

EVIDENCE OF SETTING

Table 1 summarizes the results of all known reports of oysters other than those accounted for by known introductions. In the few cases where oysters were reported by persons other than federal or state biologists, specimens were obtained and identification verified.

During most of the 11-year period, reports of oysters resulted from chance observation or from casual searches. Data for 1957, 1958, 1961, and 1962, however, were obtained by means of systematic search.

The first such systematic search was conducted in Boothbay Harbor in June 1957. At low tide, two men in a skiff examined the clearly visible portion of the bottom from mean low water to a depth of minus 4 feet (datum is mean low water) in a 2.4-mile band, averaging 30 feet in width, extending around the three major coves in the western and northern portion of the harbor (Fig. 3). Where conditions of visibility permitted, the survey occasionally included depths to approximately minus 8 feet.

In addition to the numbers of oysters given in Table 1, the results of the survey showed that: 1) only occasional small dead oysters were found between mean low water and the minus 2-foot level of extreme low tides; 2) most oysters were found in the minus 2- to minus 4-foot unexposed zone, where gravel, shell, and other firm substrate are commonly available, and 3) oysters at greater depths were found only in the rare instances where firm substrate existed.

In October 1958, during a period of extremely low tides, a more thorough survey was conducted using essentially the same methods as in 1957. In addition to examining the submerged bottom by boat, the exposed intertidal zone was explored on foot. The areas surveyed included a 1.2-mile section of the west shore of Boothbay Harbor, the area between Southport and Capitol Islands, and the northeastern portion of Linekin Bay.

This survey was carried out to gain more information on the relative abundance of oysters in the occasionally exposed zone between mean low water and minus 2 feet; and in the unexposed zone between

Table 1. Observations of progeny of European oysters in Maine, 1952-1962

	Number of oysters										
Location	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
Casco Bay											
Basin Cove	0	0	0	-	-	-	-	-	0	-	2
Bailey Island	-	-	-	-	-	-	-	1	-	-	-
Little Yarmouth Island	-	-	-	-	-	-	-	-	2	-	-
Brighams Cove	-	-	-	-	-	-	-	1	-	-	-
Small Point	-	-	-	-	-	-	-	-	-	-	3
Boothbay Harbor Area											
Hodgdon Cove	-	Few	-	-	-	-	-	-	-	2	-
Boothbay Harbor—Total	Several	91	-	Many	Many	407	920	-	-	1,250	-
West Side	Several	91	-	-	-	322	920	-	-	1,032	-
North End (2 coves)	-	-	-	-	-	85	-	-	-	218	-
Capitol Island	-	-	-	-	-	-	20	-	-	32	-
Linekin Bay—Total	-	-	-	2	12	58	586	-	-	753	-
Cove, West Side	-	-	-	2	12	-	-	-	-	537	-
North End	-	-	-	-	-	-	558	-	-	48	-
Cove, Northeast Side	-	-	-	-	-	58	28	-	-	118	-
Little River	-	-	-	-	-	-	-	-	-	-	14

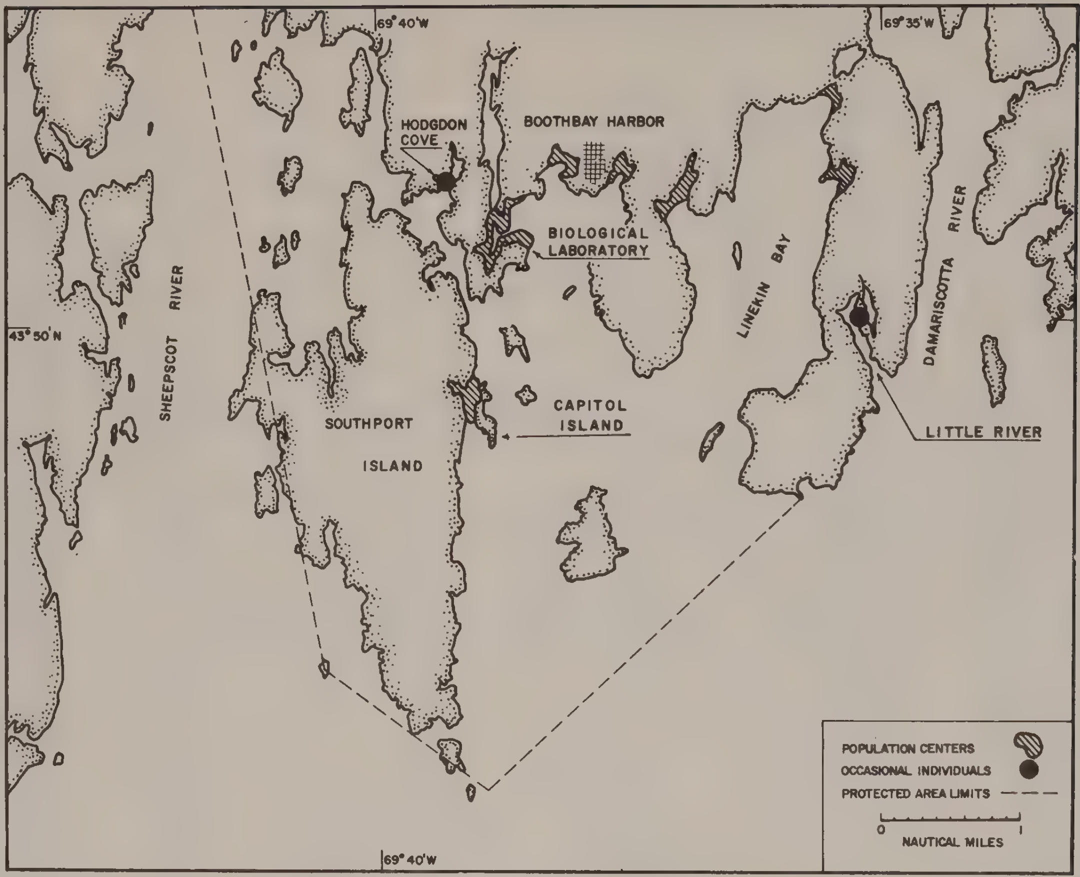
69° 40'W
69° 35'W
43° 50'N
69° 40'W
HODGDON COVE
BOOTHBAY HARBOR
BIOLOGICAL LABORATORY
LINEKIN BAY
DAMARISCOTTA RIVER
SHEEPSCOT RIVER
SOUTHPORT ISLAND
CAPITOL ISLAND
LITTLE RIVER
POPULATION CENTERS
OCCASIONAL INDIVIDUALS
PROTECTED AREA LIMITS
0
1
NAUTICAL MILES

Fig. 3. Known locations of European oysters in the Boothbay Harbor region and extent of the area within which they are protected by law.

minus 2 and minus 4 feet. Observations were also made on the relative abundance of spat, yearlings, and older oysters in the same two zones.

Total count of oysters in each area are shown in Table 1. In addition, Table 2 gives the number of oysters in each of the two bottom zones and in each of the three-year class groups. The data confirm the observation made in 1957 that abundance is generally very low in the 0- to minus 2-foot zone subject to periodic exposure. The Boothbay Harbor data, however, indicate that setting does sometimes occur in this zone.

Table 2. Results of survey of European oysters in the vicinity of Boothbay Harbor, Maine, October 1958

Location	Year Class	Number of oysters From 0 to -2 feet	Number of oysters From -2 to -4 feet
Boothbay Harbor	1958	3	0
	1957	19	16
	Older	58	824
Capitol Island	1958	0	0
	1957	0	0
	Older	0	20
Linekin Bay	1958	0	63
	1957	0	128
	Older	0	395
Total		80	1,446

Table 1 shows that the 1958 total for Boothbay Harbor is nearly three times that for the comparable area in 1957. The increase was not a result of the 1958 setting, since Table 2 shows that the greatest proportion of the oysters had set prior to 1957. Many oysters were undoubtedly overlooked in 1957 but counted during the more intensive search in 1958.

All data for 1961 and Little River data for 1962 were obtained through survey methods similar to those used in 1958, except that only total counts for each area were obtained. The two young oysters found in Basin Cove in 1962 were located by a cooperating group of SCUBA divers who searched for 13 1/2 man-hours in the subtidal zone of the cove.

EXPERIMENTAL SHELL PLANTING

During 1959 and 1960 an experiment was conducted in shell planting in Boothbay Harbor and Linekin Bay to gain information on the use of cultch and the success of setting. On 19 June and 10 July, while daily mean water temperatures were still below the minimum for spawning (Fig. 4), samples of gonads from Boothbay Harbor oysters were found to be insufficiently developed for spawning. On 22 July, after daily mean water temperatures had been above 15 C for 5 days, all six oysters of a Boothbay Harbor sample spawned soon after being placed in standing water in trays in the laboratory. On 5 August, a sample of six Boothbay Harbor oysters included three which had spawned but no longer contained larvae and three which contained black or well-advanced larvae in the mantle cavity, nearly ready to be released into the water. With the prospect of additional spawning and swarming, and, according to Korringa (1940), possible setting in 2 to 3 weeks at the prevailing temperatures, cultch was placed as follows:

On 11 to 13 August in each of two coves, one on the west side of Boothbay Harbor, the other at the northeast tip of Linekin Bay, 40 to 50 shell bags filled with soft-shell clam cultch were placed on bottom between mean low water and minus 3 feet. Approximately 4 bushels of loose clam shells were scattered just below the zone where the shell bags were placed. Seven strings, 6 to 8 feet long, of hard clam shells were suspended from a raft in Boothbay Harbor.

The cultch was examined occasionally to determine when the first set occurred, but none was found until 9 September. The first spat, two in number, were from Linekin Bay shell bags and measured 2.0 and 3.5 mm.

The final examination of cultch for the season was made during October to determine the success of setting. Five shells were removed from each shell bag for examination, and the shell bags were then moved into deeper water, well below the extreme low tide level, for protection from winter air temperatures. All of the shells on the remaining five raft-suspended strings (two had been lost) were examined. Those shells having spat on them were returned to the raft and left

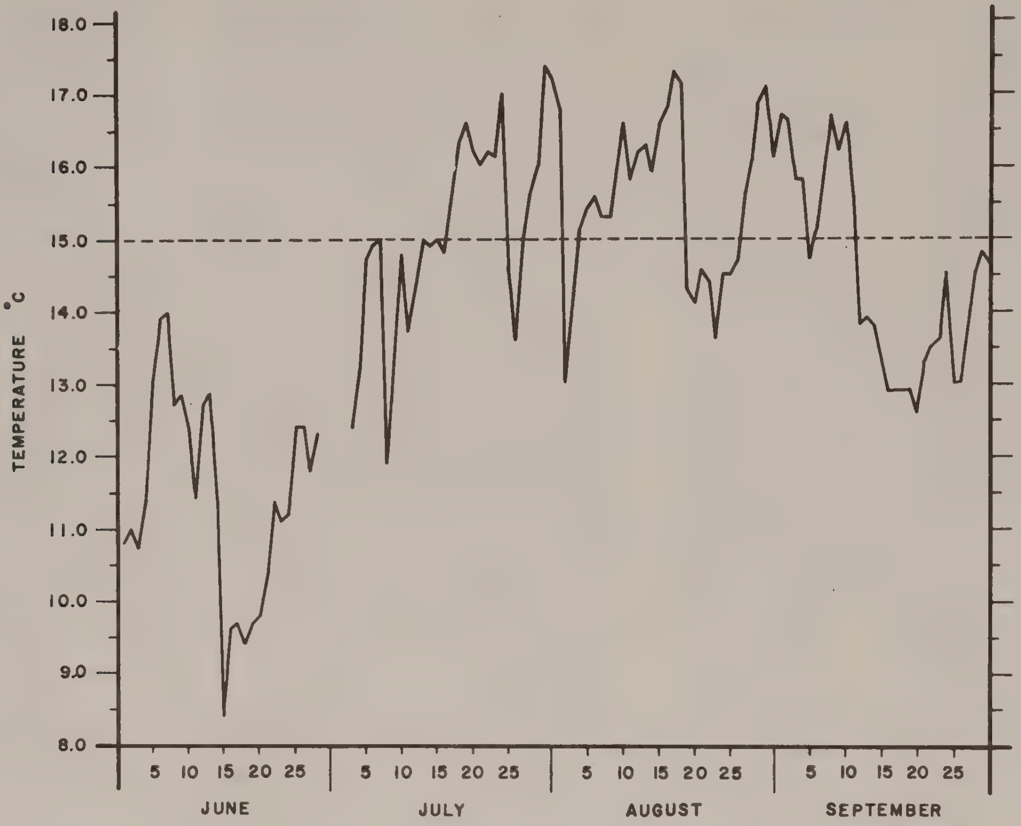

Fig. 4. Daily mean sea water temperatures at Boothbay Harbor, Maine, from June through September 1959. Dashed line at 15.0C is minimum temperature for Ostrea edulis spawning.

suspended through the winter. The loose shell on bottom was sampled, but since no set was found and the shells were heavily silted, no further examinations were made.

The results of the shell counts are shown in Table 3. The data indicate: 1) the success of setting of cultch in shell bags in Linekin Bay was of the same order of magnitude as that in Boothbay Harbor, which had been regarded as both the center of the spawning population and the area of heaviest setting; 2) the success of setting on raft-suspended shell strings was less than half as great as on cultch in shell bags in the immediate vicinity (shell strings had accumulated far more silt and fouling organisms than had the shell in bags), and 3) ranges in size were typical of set occurring over an extended period of time.

Table 3. Setting of European oysters in the vicinity of Boothbay Harbor, Maine, October 1959

Type of cultch and location	No. of shells examined	No. of spat	Ratio, spat per 100 shells	Size (mm)		
				Min.	Max.	Mean
Shell bags in Boothbay Harbor	210	97	46.2	1	13	—
Shell bags in Linekin Bay	220	115	52.3	1	10	—
Shell strings in Boothbay Harbor	105	23	21.9	3	15	6

During the following June and July (1960), the shell strings and all the shell bags that could be found were retrieved to obtain data on survival and size of the spat. As Table 4 indicates, the spat in shell bags in both Boothbay Harbor and Linekin Bay suffered extremely heavy mortalities. The spat on the raft-suspended shell strings fared better, with nearly half surviving. Percentage survival was based on the number of spat per 100 shells in October 1959 (Table 3).

The shell bags had been placed at a level where, although totally submerged, they were subjected to wave action at low tide. All shells were practically devoid of animal or plant growth. The abrasive action of the shells scouring each other and the turbidity in this zone of wave disturbance may have contributed to the mortality of spat.

Table 4. Survival and size of European oyster spat after one winter in the vicinity of Boothbay Harbor, Maine, June-July, 1960

Type of cultch and location	No. of shells examined	No. of spat	Ratio, spat per 100 shells	Survival %	Size (mm)		
					Min.	Max.	Mean
Shell bags in Boothbay Harbor	3,972	108	2.7	5.8	3	26	8
Shell bags in Linekin Bay	3,045	11	0.4	0.8	4	14	8
Shell strings in Boothbay Harbor	105	10	9.5	43.4	4	11	7

DISCUSSION

The successful culture of the European oyster could be economically important to northern New England. As far as is known, the American oyster, Crassostrea virginica, exists in New England north of Cape Cod only in the Piscataqua River between New Hampshire and Maine; in a single, small bed in the upper Sheepscot River estuary in Maine; and as rarely-found individuals in the Damariscotta River in Maine. Ecological conditions apparently do not permit spawning nor survival of larvae or spat outside these areas. Except for the bay scallop (Aequipecten irradians) just north of Cape Cod, the soft-shell clam (Mya arenaria) and the hard clam (Mercenaria mercenaria) are the most important commercially-used mollusks living in the intertidal or shallow subtidal environments. Both of the latter species are generally most abundant in areas not suitable for oysters; therefore, the ecological competition of the oyster with these species appears to be negligible.

The fact that Ostrea edulis has lived and reproduced successfully in the Boothbay Harbor, Maine area since 1949 indicates that the environment is basically suitable. Water temperature has been sufficiently high to bring about annual spawning, since setting has occurred each year, and the range of salinities observed in the area does not seem to constitute a problem. However, since the oyster population has yet to reach commercial abundance and the rate of recruitment appears to be low, there is need for a better understanding of the ecological requirements of the species and its adaptibility in the area. It should be noted that introductions of Ostrea edulis from Conway, North Wales, into Canada at St. Andrews, New Brunswick, and Ellerslie, Prince Edward Island, were made in 1957, 1958, and 1959. This move was encouraged in part by the success of the Maine introductions, but extremely heavy mortalities occurred, apparently associated with low winter water temperatures (Medcof, 1961).

In Maine the results of the 1957 and 1958 surveys indicate the existence of two conditions which seriously limit the increase in oyster abundance. First, the relative scarcity of oysters in the zone occasionally exposed at extreme low tides indicates that the oysters cannot withstand winter air temperatures. According to Gaarder and Bjerkan (1934), Ostrea edulis in sea water can tolerate temperatures slightly below 0C, but those exposed to freezing temperatures in air will be seriously weakened and damaged, if not killed. In northern New England, subfreezing air temperatures coincide with extreme low tides often enough to virtually eliminate the entire intertidal zone from year-round production of oysters. Second, oysters were found only on firm substrate. Unfortunately, a large proportion of the bottom examined during the surveys and most of the bottom at greater depths, was covered with silt and completely devoid of the shell, rock, or gravel necessary for setting.

A possible third limiting set of conditions is of hydrographic nature but no specific information has been obtained. Korringa (1940) indicated that Ostrea edulis set may not reach commercial quantities in areas where water temperatures are not higher than 18 C, or where tidal exchange may reduce the numbers of planktonic larvae. He pointed out that in such circumstances proper use of cultch is necessary to make maximum use of the available set. Both of these limiting conditions of temperature and tidal exchange prevail in many New England areas.

The encouraging results of the trial use of cultch in 1959 indicate that, through employment of improved methods and materials, stocks of oysters might be increased far beyond those that have accumulated under natural conditions. Suitable subtidal growing ground is limited so that raft or rack culture, or relaying, might be necessary for a commercial operation.

Over a period of 13 years, sufficient encouragement has been gained from observations of the natural growth of the oyster population in the Boothbay Harbor area to recommend that further research be conducted on the European oyster. A research program should include:

1) determination of the physiological requirements of the oyster; 2) ecological studies of areas where the oyster has become established; 3) determination of the setting potential and satisfactory use of cultch, and 4) determination of the degree of physiological adaptation of the Dutch strain of *Ostrea edulis* to Maine waters since it was first introduced.

Future growth of the oyster population and any possible future research will be aided by the protection now afforded the species in the Boothbay Harbor area. In June 1960 the Maine Department of Sea and Shore Fisheries recognized the potential importance of this oyster and established an extensive closed area (Fig. 3), within which the taking of European oysters is forbidden by law. The boundaries of the closed area include all major known populations and the localities where continued spread and increase in abundance may be expected.

CONCLUSIONS

1. Temperature and salinity characteristics of parts of the Maine coast are basically suitable for survival, growth, and reproduction of *Ostrea edulis* from Holland.

2. In the Boothbay Harbor, Maine area, oysters have spawned and set annually since 1949 and numbers and range have shown progressive increases.

3. The greatest numbers of progeny exist only in the zone below the range of extreme low tides.

4. Mortality caused by low winter air temperatures is believed to limit abundance of oysters in the intertidal zone, and setting at lower levels is limited by a scarcity of suitable substrate.

5. More set occurred in shell bags on bottom than on raft-suspended shell strings, but winter and spring survival was better on the shell strings.

6. The persistent increases and spread of the Boothbay Harbor oyster population warrants further research.

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Seasonal and Depth Distribution of Larval Bloaters (*Coregonus hoyi*) in Southeastern Lake Michigan

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Seasonal and Depth Distribution of Larval Bloaters (*Coregonus hoyi*) in Southeastern Lake Michigan

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ABSTRACT

Larvae of bloaters (*Coregonus hoyi*) were sampled systematically in southeastern Lake Michigan, off Saugatuck, Michigan, from 9 April to 22 August 1964; limited additional sampling was done on 15 October. All collections were made with a 1-m plankton net of 0.66-mm mesh. A standard series of samples consisted of oblique tows for each 10-fathom (sometimes 5-fathom) stratum over bottom depths from 5 to 50 fathoms by 5-fathom intervals. Some additional oblique tows were made at 60, 70, 80, and 88 fathoms, and a single day–night series of horizontal tows was made at 40 fathoms.

Few bloater larvae were taken when sampling began in early April. Numbers increased steadily thereafter until late June and early July, after which the catch declined rather rapidly. Few were caught on 22 August and none on 15 October. Hatching appeared to be at its peak about mid-June.

Approximately 83% of all bloater larvae were taken where the lake was between 40 and 60 fathoms deep. The depth of greatest abundance appeared to be between 50 and 60 fathoms. Larvae were present at all depths sampled except at 5 fathoms, but were scarce in areas 10, 15, and 20 fathoms deep. Most were found near bottom, except during the April and early May collections. About 96% were taken from strata in which the maximum temperature was not more than 4.7 C. There was evidence that weak swimming ability of the larvae as well as water temperature influenced vertical depth distribution. A limited but definite upward vertical migration occurred at night.

INTRODUCTION

The bloater (*Coregonus* [*Leucichthys*] *hoyi*) has been the most important commercial fish species in Lake Michigan in recent years. No statistics of bloater catches are available, because it is one of several deepwater ciscoes (*Coregonus* [*Leucichthys*] spp.) which are marketed collectively as "chubs." Bloaters, however, have constituted practically the entire chub catch of Lake Michigan in recent years (Moffett, 1957; Smith, 1964). The average annual production of chubs in Lake Michigan in 1955–64 was about 10 million pounds.

The bloater has been the subject of considerable investigation in Lake Michigan, mostly by the U. S. Bureau of Commercial Fisheries. Published reports have included descriptions of: taxonomy (Koelz, 1929); age, growth, and bathymetric distribution (Jobes, 1949); population changes (Moffett, 1957; Smith, 1964); and food (Wells and Beeton, 1963). Nothing has been published on bloater larvae, or larvae of any of the deepwater ciscoes of North America. This study provides information on a phase in the life history of the Lake Michigan bloater about which little is known.

METHODS AND MATERIALS

Sampling was conducted from the U. S. Bureau of Commercial Fisheries R/V *Cisco*. Collections were made off Saugatuck, Michigan, with a 1-m plankton net of 656 Nitex (0.66-mm mesh). This mesh was sufficiently small to catch bloater larvae, yet large enough to permit good passage of water. The net ring was mounted in a 1-m square frame with a bridle attached so that there was no obstruction ahead of the opening. This bridle arrangement was identical to one on a 5-ft frame used at the Scripps Institution of Oceanography (Blackburn and Reith, 1962). A 45-lb brass depressor was attached to the bottom of the frame at the center. The net and frame were green, to minimize contrast with the water and reduce visibility to fish larvae. The net was towed with a ⅝-inch cable at a speed of 3.5 knots. Vessel speed was kept constant by varying the engine speed to maintain a constant wire angle.

Series of samples were taken at intervals of about 10 days from 9 April to 22 August 1964. A few tows were made on 15 October. A standard series of samples consisted of oblique tows at stations located at 5-fathom intervals of bottom depth from 5 to 50 fathoms. The oblique tows at each station were made by 10-fathom strata, except at depths not multiples of 10 fathoms (5, 15, . . . fathoms), where the lowermost stratum was only 5 fathoms.

For an "oblique tow" the net, as it was lowered, was towed 1 min at each of 11 equally spaced levels in the upper 55 ft of the 10-fathoms stratum being sampled, and then brought up at constant speed. For 5-fathom strata the net was towed for 1 min at five levels—four equally spaced in the upper 22 ft and the other at 25 ft. Thus the lowermost 5 ft were not sampled in any stratum, and the danger of striking bottom in the lowest strata was minimized. The times required to sample 10-fathom and 5-fathom strata averaged 15.4 and 8.5 min, respectively. No flowmeter was used, but since the towing times varied only slightly, and clogging of the relatively large mesh was not a problem, it is assumed that the volumes strained in either 5- or 10-fathom strata did not differ significantly.

During all tows the wire angle was 20° from the horizontal. Depth was regulated by the amount of wire out and was occasionally checked with a depth recorder. The depth recorder showed that about 3.5% more wire was required to place the net at a specified depth than was calculated from the wire angle.

Fourteen "standard series" of tows were made during the study. Nine were complete (all strata sampled), two lacked a few tows, and the remaining three were incomplete to a considerable degree. It usually required 3 days to complete a series over all bottom depths from 5 to 50 fathoms. All strata of a given station were always sampled on the same day. After the completion of a standard series, collections were usually made in selected strata at 60 fathoms and occasionally at 70, 80, and 88 fathoms. These samples are grouped with the standard series which they followed; collection periods mentioned in this report, however, include only the dates required to complete the standard series. A single day–night series of horizontal tows was made at 40 fathoms.

After each tow the fish larvae were sorted by species, counted immediately, and preserved in 10% formalin. Most larvae other than ciscoes were alewives (*Alosa pseudoharengus*) and cottids (probably *Myoxocephalus quadricornis* and *Cottus cognatus*).

It was not possible to identify the cisco larvae to species, but the adult cisco population of southeastern Lake Michigan at the time of this study was so predominantly bloater (99.2% during 1964 in experimental trawl catches) that all cisco larvae have been considered bloaters with little fear of significant error.

A portion of the bloater larvae from the first standard series, and from alternate series thereafter, was measured in the laboratory. In samples containing 10 or fewer larvae, all were measured; in samples containing more than 10, a random subsample of 10 was measured. Usual methods of measurement were not used because many of the larvae were bent or curled. Lengths of the larvae were obtained by measurement of images on the screen of a microprojector used to read fish scales (Moffett, 1952). The length of the image (magnification 27.6×) was traced on a strip of translucent paper and measured to the nearest millimeter with a map measurer. Actual lengths were obtained by application of a factor of 0.0362 (= 1/27.6) and rounded to the nearest 0.1 mm. Larvae in the standard series that were measured were separated into those with a conspicuous yolk sac and those without a yolk sac.

ADJUSTMENT OF CATCH FIGURES

Actual catches (Table 1) in the standard series (5 to 50 fathoms) were adjusted (Table 2) to make all figures comparable. Since the net lacked an opening–closing device, it frequently passed through strata above those being specifically sampled. Additional larvae were caught as the net passed through these strata but the number should have been small for most hauls because bloater larvae were usually sparse in the upper levels. Corrections made for this contamination were calculated for each series on the assumption that the time the net was in a given stratum was proportional to the catch in that stratum. The time required to sample a 10-fathom stratum was 15.4 min (1 min at each of 11 levels, and

TABLE 1.—*Number of bloater larvae taken in oblique tows in different strata at various bottom depths and dates*

Bottom depth (fathoms)	Stratum (fathoms)	9–12 April	18–20 April	29 April–1 May	8–11 May	20–22 May	28–30 May	11–13 June	19–22 June	1–3 July	9–11 July	22–24 July	30 July–1 Aug.	13–14 August	22 August
5	0– 5	0	0	0	0	0	0	0	0	0	0	0	0	0	—
10	0–10	—	0	0	0	0	0	1	0	0	0	0	1	0	—
15	0–10	0	1	2	0	0	0	0	0	0	0	0	2	0	—
	10–15	1	0	0	1	0	0	1	1	0	0	0	1	0	—
20	0–10	0	1	3	0	0	0	0	0	0	0	0	1	0	—
	10–20	0	1	0	0	0	0	5	1	1	3	0	1	0	—
25	0–10	0	0	0	3	0	0	0	—	1	—	0	1	2	—
	10–20	0	0	3	4	0	0	0	—	1	3	0	1	0	—
	20–25	0	0	0	1	0	0	8	—	7	3	3	6	0	—
30	0–10	1	0	3	1	0	0	0	—	1	0	0	0	0	—
	10–20	1	1	1	2	0	0	0	—	1	0	1	2	0	—
	20–30	0	0	3	0	0	0	6	6	18	14	5	4	0	—
35	0–10	2	3	1	3	2	0	0	—	1	—	1	1	0	—
	10–20	0	0	1	1	1	0	0	—	6	—	0	0	0	—
	20–30	0	0	5	1	9	2	1	—	5	4	11	3	0	—
	30–35	0	0	5	2	5	12	22	—	14	19	8	8	0	—
40	0–10	0	1	1	3	4	0	0	—	1	—	0	0	0	—
	10–20	0	0	3	2	4	0	0	—	8	—	1	2	0	—
	20–30	0	1	2	4	4	2	5	5	10	3	3	5	1	—
	30–40	0	0	1	—	24	8	17	79	62	14	15	15	1	—
45	0–10	1	3	1	2	2	1	0	—	0	—	1	0	0	—
	10–20	0	1	0	5	2	1	0	—	1	—	0	1	1	—
	20–30	0	2	1	16	1	2	1	—	9	—	10	2	1	—
	30–40	0	1	9	11	11	3	35	—	10	34	29	10	6	1
	40–45	0	2	8	—	20	35	67	—	37	67	75	10	5	3
50	0–10	1	0	11	10	2	2	0	0	0	—	2	3	0	—
	10–20	1	1	1	2	2	1	0	1	0	—	2	0	2	—
	20–30	0	—	6	8	2	0	0	4	3	—	3	5	2	—
	30–40	2	—	11	7	13	9	5	7	30	13	19	8	3	1
	40–50	0	—	27	22	25	65	68	57	81	42	49	36	4	4
60	0–10	—	1	12	—	5	2	0	—	—	—	1	—	—	—
	10–20	—	1	2	—	—	—	—	—	—	—	0	—	—	—
	20–30	—	—	—	—	—	—	—	—	—	—	0	—	—	—
	30–40	—	—	—	—	—	—	—	—	—	—	10	—	1	—
	40–50	—	—	—	—	—	—	—	—	4	15	16	15	11	5
	50–60	—	—	—	—	75	78	85	—	17	27	19	24	9	1
70	0–10	—	—	11	—	8	1	0	—	—	—	—	—	—	—
	10–20	—	—	1	—	—	—	—	—	—	—	—	—	—	—
	20–30	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	30–40	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	40–50	—	—	—	—	—	—	—	—	—	—	—	—	2	—
	50–60	—	—	—	—	—	—	—	—	—	—	5	—	3	—
	60–70	—	—	—	—	1	19	3	—	—	24	4	12	4	—
80	0–10	—	—	4	—	3	1	0	—	—	—	—	—	—	—
	10–20	—	—	2	—	—	—	0	—	—	—	—	—	—	—
	70–80	—	—	—	—	4	15	2	—	—	—	—	—	—	—
88	0–10	—	—	4	—	—	—	—	—	—	—	—	—	—	—
	10–20	—	—	2	—	—	—	—	—	—	—	—	—	—	—

4.4 min between steps and to bring the net back up through the stratum). The total time to pass a net down and up through strata not being sampled averaged 3.7 min (1.0 min down, 2.7 min up). Thus, the larvae caught as the net passed through a stratum not being sampled were considered as 24% (3.7/15.4) of the catch (adjusted) in that stratum when it was actually sampled. Therefore, the catch in any tow was reduced by 24% of the adjusted catches that were made in each higher level.[1]

When certain strata in the upper levels were

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[1] Example: Assume the actual catches in the three strata of the station at 30 fathoms were 4, 5, and 25. There would be no adjustment for the uppermost sample. The adjusted catch from the second stratum would be $5 - 0.24(4) = 4$ (rounded to the nearest whole fish). The adjusted catch from the lowermost stratum would be $25 - 0.24\ (4 + 4) = 23$.

TABLE 2.—*Adjusted catches of bloater larvae taken in standard series*

Bottom depth (fathoms)	Distance from shore (miles)	Stratum (fathoms)	9–12 April	18–20 April	29 April–1 May	8–11 May	20–22 May	28–30 May	11–13 June	19–22 June	1–3 July	9–11 July	22–24 July	30 July–1 Aug.	13–14 August	22 August	Total for all strata[1]
5	0.5	0–5	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0
10	2.0	0–10	—	0	0	0	0	0	1	0	0	0	0	1	0	—	2
15	3.5	0–10	0	1	2	0	0	0	0	0	0	0	0	2	0	—	
		0–15	1	0	0	1	0	0	1	1	0	0	0	1	0	—	7
20	4.5	0–10	0	1	3	0	0	0	0	0	0	0	0	1	0	—	
		10–20	0	1	0	0	0	0	5	1	1	3	0	1	0	—	11
25	5.5	0–10	0	0	0	3	0	0	0	—	1	—	0	1	2	—	
		10–20	0	0	3	3	0	0	0	—	1	3	0	1	0	—	
		20–25	0	0	0	1	0	0	7	—	6	2	3	5	0	—	30
30	7.0	0–10	1	0	3	1	0	0	0	—	1	0	0	0	0	—	
		10–20	1	1	0	2	0	0	0	—	1	0	1	2	0	—	
		20–30	0	0	2	0	0	0	6	6	18	14	5	4	0	—	45
35	8.0	0–10	2	3	1	3	2	0	0	—	1	—	1	1	0	—	
		10–20	0	0	1	0	1	0	0	—	6	—	0	0	0	—	
		20–30	0	0	5	0	8	2	1	—	3	4	11	3	0	—	
		30–35	0	0	3	1	2	11	20	—	11	16	5	6	0	—	107
40	10.0	0–10	0	1	1	3	4	0	0	—	1	—	0	0	0	—	
		10–20	0	0	3	1	3	0	0	—	8	—	1	2	0	—	
		20–30	0	1	1	3	2	2	5	5	8	3	3	5	1	—	
		30–40	0	0	0	—	22	8	16	78	58	13	14	13	1	—	182
45	15.0	0–10	1	3	1	2	2	1	0	—	0	—	1	0	0	—	
		10–20	0	0	0	5	2	1	0	—	1	—	0	1	1	—	
		20–30	0	1	1	14	0	2	1	—	9	—	10	2	1	—	
		30–40	0	0	9	6	10	2	35	—	8	34	26	9	6	1	
		40–45	0	1	5	—	15	31	52	—	30	53	60	6	3	3	345
50	19.0	0–10	1	0	11	10	2	2	0	0	0	—	2	3	0	—	
		10–20	1	1	0	0	2	1	0	1	0	—	2	0	2	—	
		20–30	0	—	3	5	1	0	0	4	3	—	2	4	2	—	
		30–40	2	—	8	3	12	8	5	6	29	13	18	6	2	1	
		40–50	0	—	23	18	21	62	67	54	73	39	43	33	3	4	459
Total			10	21[2]	89	105[2]	111	133	222	—	278	218[2]	208	113	24	16[2]	

[1] Totals at each bottom depth are combined catches of all strata for the nine completed series: 9–12 April; 29 April–1 May; 20–22 May; 28–30 May; 11–13 June; 1–3 July; 22–24 July; 30 July–1 August; 13–14 August.

[2] Total includes an adjustment for the missing tows. See text for explanation of method of making adjustments.

not sampled, calculations were not possible. The 19 to 22 June series lacked so many samples that it was eliminated from consideration in most comparisons. In the others contamination was almost certainly slight and was ignored.

A second adjustment made the catches in the 5-fathom strata proportional to those in the 10-fathom strata. The sampling time in 5-fathom strata (8.5 min) was somewhat more than half that of the 10-fathom strata (15.4 min), so a correction factor (0.905) was applied to all catches in 5-fathom strata. This adjustment assumes that, given equal distribution, the total number of larvae within a 5-fathom stratum should be one-half the number in a 10-fathom stratum.

For analysis of seasonal changes in abundance, the total catches of standard series containing missing tows had to be adjusted to make them comparable. The adjustments were made on the basis of comparison of the tows acutally made with catches of corresponding tows of the series immediately preceding and immediately following. The procedure is presented for an actual case: The second series (18 to 20 April) lacked the three tows nearest bottom at 50 fathoms (Table 2). The first and third series (9 to 12 April and 29 April to 1 May) were complete.[2] The catches from tows of the first and third series which corresponded to the tows completed in the second series constituted

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[2] The first series lacked the single tow at 10 fathoms, but it is assumed that no bloater larvae would have been caught had the tow been made, since only two were taken at this depth during the entire season (the first one in mid-June).

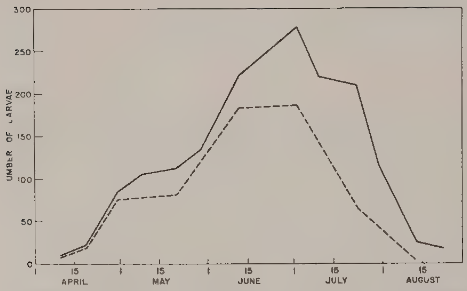

FIGURE 1.—Total number of bloater larvae (solid line) and number of larvae with yolk sacs (broken line) collected in standard series on different dates. The number of larvae with yolk sacs was determined for alternate collections; the value for mid-April (18 to 20) was derived from the mean percentage of larvae with yolk sacs in collections of 9 to 12 April and 29 April to 1 May.

80.0 and 61.8% of the catch of all tows, respectively. It was assumed that the catch of completed tows in the second series would have been the average of these (70.9%); the estimated total catch was obtained by multiplying the actual catch by 1.41 (1/0.709). Fifteen larvae were caught in the second series, and the adjusted catch was 1.41 × 15 = 21. A similar adjustment was made for the series of 8 to 11 May, 9 to 11 July, and 22 August. The adjustment for the 22 August series was based solely on the preceding series, since none followed. The series of 19 to 22 June lacked samples at many levels at which larvae were probably numerous, so no estimate was made.

SEASONAL CHANGES IN ABUNDANCE

Few bloater larvae were present when sampling began on 9 April. The catches increased steadily thereafter until a peak was reached in early July, after which numbers of larvae declined rather rapidly (Table 2, Figure 1). Few remained on 22 August, and none were caught on 15 October. It is possible that the 19 to 22 June series, had it been complete, would have had the largest total. If all levels at the depth of 60 fathoms had been sampled sufficiently to include this important depth (discussed in a later section) in the standard series, the largest total catch almost surely would have occurred in June. The catch at 60 fathoms was largest in mid-June, and dropped sharply by early July.

Although information on larval growth is lacking, evidence suggests that most larvae were so young at capture that the seasonal abundance of the bloater larvae should reflect the hatching season. This evidence is described below.

It seems improbable that any of the bloater larvae were small enough to escape through the meshes of the net. Well-developed larvae removed from eggs which had been picked up from the bottom appeared much too large to pass through the 0.66-mm mesh. One of these larvae was 10.0 mm long (no others were measured).

The length distribution of the bloater larvae taken in the nets changed little throughout the season. Average lengths of larvae taken during alternate collection periods from April to August were 11.3, 11.0, 11.0, 11.0, 11.3, 11.1, and 11.2 mm (Table 3). The smallest was 8.6 mm and the largest 14.9 mm; 60 to 86% (average 75%) of those caught in the various periods were 10.0 to 11.9 mm. The percentages of larvae with yolk sacs from April to August were 70, 83, 72, 82, 67, 32, and 18 (Table 3). The fish without yolk sacs averaged 11.5 and 11.3 mm in the 29 April to 1 May and 22 to 24 July sampling periods, respectively, whereas those with yolk averaged 10.8 mm in both periods. The fish without yolks may have completed absorption of the yolk shortly before capture, since they were only slightly larger than those with yolk. Lake Michigan bloaters grow approximately 100 mm (total length) in the first year according to back calculations from bloater scales collected during the R/V *Cisco* operation in 1964. It seems probable, therefore, that they pass quickly through the 10- to 12-mm size range of most fish taken in this study.

The unchanging length composition, the presence of many larvae with yolk sacs, and the small size of the larvae caught compared with the size at the end of the first year, are evidence that most larvae captured were very young throughout all sampling periods, and that the changes in catch must have followed closely the progress of hatching. The fish apparently were able to escape the net soon after absorption of their yolk sacs. No coregonid fry beyond the earliest stages have been taken in plankton or fry-net tows which

TABLE 3.—*Length distribution (percentage) of bloater larvae and number of larvae with and without yolk sacs in various periods*

Length (mm)	9–12 April	29 April–1 May	20–22 May	11–13 June	1–3 July	22–24 July	13–14 August
8.0– 8.9	—	0.9	—	—	—	—	—
9.0– 9.9	10.0	5.8	16.7	7.6	6.6	5.9	10.7
10.0–10.9	20.0	45.2	43.6	54.0	26.7	33.0	34.5
11.0–11.9	40.0	33.2	22.0	31.6	51.7	51.4	34.2
12.0–12.9	30.0	14.9	12.9	6.4	12.4	9.7	16.0
13.0–13.9	—	—	3.0	0.4	—	—	3.6
14.0–14.9	—	—	1.9	—	2.6	—	—
Number of fish[1]	10	109	133	242	308	238	28
Average length	11.3	11.0	11.0	11.0	11.3	11.1	11.2
Percentage with yolk sacs	70	83	72	82	67	32	18
Number with yolk sacs[2]	7	74	80	182	186	67	4

[1] Not adjusted, therefore numbers are larger than in Table 2 (except in the 9–12 April series for which no adjustments were necessary).

[2] Calculated by multiplying percentage with yolk sacs by total catches in Table 2, which had been adjusted for contamination.

have been made by the Bureau of Commerical Fisheries throughout the Great Lakes since 1950, and there is no evidence in the literature that others have been able to catch them.

Hatching must have begun soon before 9 April because few larvae were taken in the first sampling period, and 70% of these had yolk sacs (Table 3). The peak catches of fish with yolk sacs were during 11 to 13 June (182 fish) and 1 to 3 July (186 fish), after which catches declined sharply until only four were taken during 13 to 14 August (Figure 1). If the catches from 60 fathoms, where hatching is apparently somewhat earlier, had been included with these data, the peak of hatching would be shown as about mid-June.

Evidence from experimental gill nets and trawls fished by the Bureau of Commercial Fisheries indicates that the spawning season of bloaters in Lake Michigan extends from January into March. In 1955, 11% of the bloaters caught off Grand Haven, Michigan, on 25 January had spawned; 70% had spawned by 9 March. Off Saugatuck in 1964, 40 and 96% had spawned by 13 February and 11 March, respectively. The fish at Saugatuck were caught in the same area and year as were the larvae for the present study. If it is assumed that most of the eggs were spawned from mid-January to mid-March, and hatched from mid-May to mid-July, the average incubation period appears to be about 4 months. If so, at least some of the few larvae caught in April may have come from eggs laid in December. The earliest bloater spawning may have occurred in that month, but it is possible that a few of the larvae taken in April were lake herring (*Coregonus artedi*), a late-November and December spawner in Lake Michigan (Koelz, 1929). This species made up about 0.5% of the ciscoes in experimental fishing off Saugatuck in 1964. Other ciscoes taken off Saugatuck in 1964 were *C. reighardi* (0.2%) which spawns in April–June, and *C. alpenae, C. kiyi,* and *C. zenithicus* (collectively 0.1%) which spawn in September–November.

DEPTH DISTRIBUTION

Bathymetric distribution

Bloater larvae were taken at all depths over which they were sampled, except 5 fathoms. Few were taken at 10, 15, and 20 fathoms; numbers became steadily larger with depth to 50 fathoms, where, on the basis of the nine completed standard series, the abundance (total larvae in all series, surface to bottom) was 459 (Table 2). The estimated abundance at 60, 70, and 80 fathoms[3] was 411,111, and 61 larvae, respectively. Although the largest catch was at 50 fathoms, the distribution with

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[3] Although sampling was limited at 60, 70, and 80 fathoms, sufficient tows were made to permit an estimate of the relative abundance at these depths. These estimates were obtained by determining the ratio of all catches in the two bottom strata (where most larvae were concentrated, as described later) at each of the deeper stations with the total catches of corresponding tows in the bottom two strata at 50 fathoms for the various sampling periods, and applying the ratio to the relative abundance at 50 fathoms (459 larvae). Too few samples were taken at 88 fathoms to estimate abundance, but it probably was low.

TABLE 4.—*Number and percentage of bloater larvae caught in each 10-fathom stratum, at stations with bottom depths of 30, 40, and 50 fathoms. Figures represent totals from nine complete standard series*

Stratum (fathoms)	Bottom depth (fathoms) 30 Number	30 Percentage	40 Number	40 Percentage	50 Number	50 Percentage
0–10	5	11.1	6	3.3	21	4.6
10–20	5	11.1	17	9.4	8	1.7
20–30	35	77.8	27	14.8	15	3.3
30–40	—	—	132	72.5	90	19.6
40–50	—	—	—	—	325	70.8

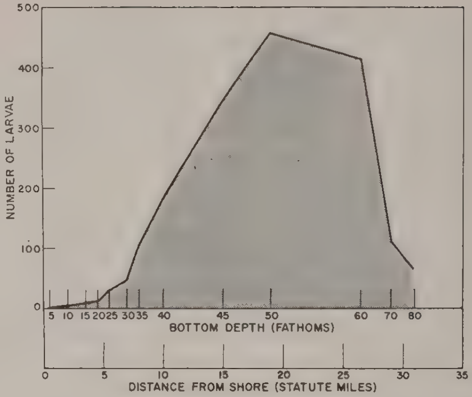

FIGURE 2.—Number of bloater larvae at various bottom depths and distances from shore. The numbers for depths from 5 to 50 fathoms are adjusted totals for nine complete standard series. The numbers for 60, 70, and 80 fathoms are relative figures, based on comparison of certain catches at those depths with corresponding catches at 50 fathoms. See text for details.

depth (Figure 2) suggests that the peak abundance may have been between 50 and 60 fathoms. The 40- to 60-fathom depth range contained both a high concentration of larvae and a substantial portion of the total sampling area (about 53% of the area between shore and 80 fathoms; see Figure 2). If it is assumed that the change in density was constant over the distance between successive sampling depths, an estimated 83% of all larvae in water 80 fathoms and shallower were between 40 and 60 fathoms. The figure would be even larger if it is assumed that peak abundance was between 50 and 60 fathoms, rather than at 50 fathoms.

Vertical distribution

The few larvae taken in the first two collection periods (9 to 12 April and 18 to 20 April) were distributed more or less evenly through all strata (Table 2). In the next two collection periods (29 April to 1 May and 8 to 11 May) the largest catches in deeper water tended to be near the bottom. Thereafter, most larvae at all depths were taken from the tows near bottom.[4] The percentages of larvae in the stratum nearest bottom at 30, 40, and 50 fathoms, calculated on the basis of the nine completed series combined, were 77.8, 72.5, and 70.8, respectively (Table 4). Corresponding percentages for tows in the uppermost stratum were 11.1, 3.3, and 4.6.

Bloater larvae were clearly in very cold water. An example of the vertical distribution of the larvae under various thermal conditions at 50 fathoms is presented in Table 5 and Figure 3, but conclusions apply generally to all depths. During the 9 to 12 April, 29 April to 1 May, and 8 to 11 May series, when an appreciable proportion of the larvae was in the upper strata, the water was cold and nearly homothermous. Only slight surface warming had occurred by 20 to 22 May, but the strong tendency to concentrate near the bottom had already developed. As surface warming continued and thermal stratification became more pronounced, the larvae became even more concentrated at the lower levels. During the June, July, and August sampling at 50 fathoms, where surface-water temperatures in this period ranged from 10.9 to 22.8 C, 95.9% of all bloater larvae were caught in strata in which the maximum temperature was less than 4.8 C.

Although these data suggest a strong preference for cold water, there is evidence that the concentration near bottom was not wholly related to temperature. The tendency for more larvae in bottom strata began when surface warming was only slight; thereafter the lowermost stratum was never more than a few tenths of a degree colder than the stratum immediately above, yet the lower

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[4] The catches (Table 2) in the lowermost tows at the odd depths (5-fathom strata) must be doubled to give indices of larval concentration comparable with the catches of the 10-fathom strata. Such a change would emphasize even more the tendency of the larvae to congregate near the bottom.

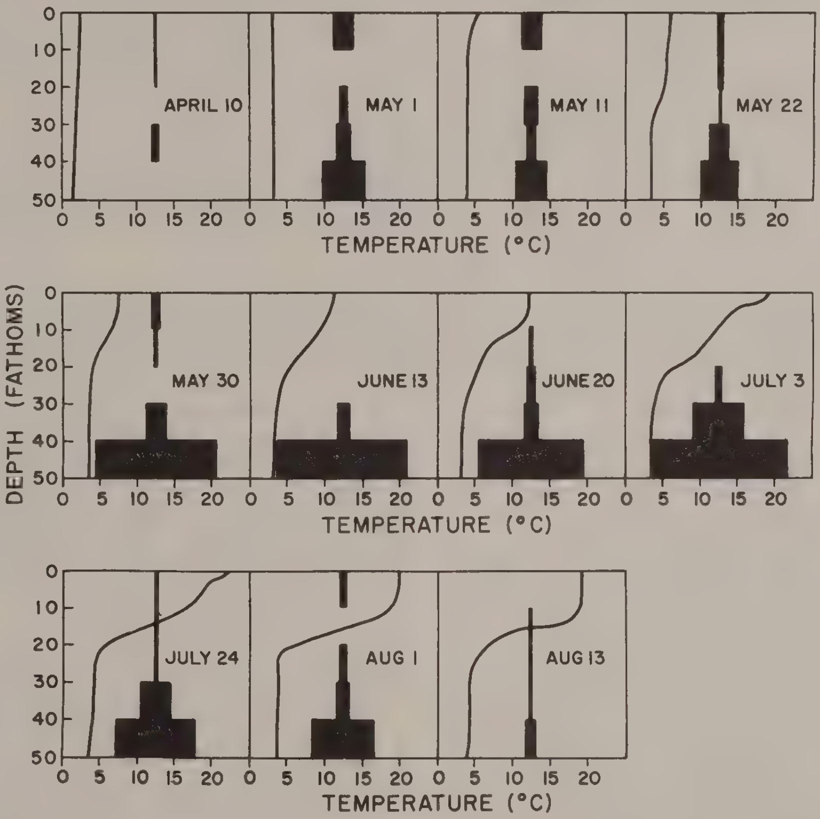

FIGURE 3.—Vertical distribution of bloater larvae and temperature profile for all dates on which a complete series was made at a bottom depth of 50 fathoms. The full width of the panel for each date represents 100 larvae.

stratum usually contained far more larvae. A possible explanation for the concentrations near bottom is found if we assume that the newly hatched larvae, with rather large yolk sacs, are unable to swim well and most occasionally rest on bottom. During the early periods, however, when homothermous conditions prevailed, the larvae might have been carried into the upper levels by the circulation of the overturn. There is also some evidence to support the belief that the young bloaters have less tendency to remain near the bottom as soon as they lose their yolk sacs and develop a stronger swimming ability. In the series in which the larvae were measured and examined for yolk sacs, 55% of the larvae in the upper 10 fathoms (at bottom depths greater than 10 fathoms) had no yolk, and their average size was 11.5 mm; for all strata deeper than 10 fathoms combined the figures were 35% and 11.1 mm, respectively. In the last five series, when the larvae were strongly bottom-oriented, 86% of the larvae in the top 10 fathoms had no yolk and averaged 11.7 mm; 38% lacked yolk sacs and the length averaged 11.1 mm in deeper strata.

TABLE 5.—*Number of bloater larvae caught and temperature (C) of various strata on dates when complete series of tows were made at a bottom depth of 50 fathoms*

[Temperature for the top of each stratum is given in parentheses]

Date	Depth (fathoms)					Bottom temperature
	0–10	10–20	20–30	30–40	40–50	
10 April	1 (2.2)	1 (2.2)	0 (2.1)	2 (2.1)	0 (2.1)	2.1
1 May	11 (3.1)	0 (3.1)	3 (3.1)	8 (3.0)	23 (3.0)	3.0
11 May	10 (4.3)	0 (4.1)	5 (3.7)	3 (3.7)	18 (3.7)	3.7
22 May	2 (5.7)	2 (5.4)	1 (4.7)	12 (3.7)	21 (3.6)	3.5
30 May	2 (7.5)	1 (6.3)	0 (4.7)	8 (4.0)	62 (3.7)	3.6
13 June	0 (10.9)	0 (9.4)	0 (5.0)	5 (4.2)	67 (3.7)	3.6
20 June	0 (11.9)	1 (10.6)	4 (4.7)	6 (4.0)	54 (3.6)	3.6
3 July	0 (19.1)	0 (12.1)	3 (6.5)	29 (4.0)	73 (3.6)	3.6
24 July	2 (22.8)	2 (15.7)	2 (4.7)	18 (4.1)	43 (4.0)	3.8
1 August	3 (19.7)	0 (19.1)	4 (4.1)	6 (4.1)	33 (4.1)	4.0
13 August	0 (19.1)	2 (18.9)	2 (6.6)	2 (4.3)	3 (4.1)	4.1

TABLE 6.—*Number of bloater larvae caught in day and night series at various levels over bottom depth of 40 fathoms*

Depth (feet)	Number of larvae	
	Day (1515–1720)	Night (2110–2340)
0	0	1
50	3	5
100	4	3
150	2	7[1]
200	5	65
230	125	46
Total	139	127

[1] Fourteen larvae were taken in a tow at 150 feet, made 1 hr and 5 min after the tow at that depth in the regular night series.

Vertical migration

Limited evidence of some vertical movement off the bottom at night was obtained on 5 July. Series of horizontal tows of 10 min each were made in the afternoon (1515 to 1720) and again at night (2110 to 2340) at 230, 200, 150, 100, and 50 ft (38.3, 33.3, 25.0, 16.6, and 8.3 fathoms) and the surface over a bottom depth of 240 ft (40 fathoms). A pronounced decrease at night in the number of bloater larvae at the lowest level (230 ft), a corresponding increase in the next level above (200 ft), and small changes at other depths (Table 6) indicated a definite movement upward at night, but for only a short distance. Larval numbers increased only slightly in a third tow at 150 ft, made 1 hr and 5 min after a previous tow at that depth in the night series; thus it appears unlikely that any appreciable movement into the upper levels took place after sampling had been discontinued. The figures in Table 6 represent actual catches and could not be corrected to eliminate fry taken as the net was lowered and brought to the surface. Error from larvae taken when lowering and raising the net should have been minor in the day series, when most larvae were at the bottom level. It may have been appreciable in the sample from the 230-ft level at night, however, because the net passed through a concentration of larvae just above. Thus, the movement upward from near the bottom was probably even more pronounced than the figures indicate.

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Tolerances of Several Marine Species to Co 60 Irradiation[1]

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ABSTRACT: Mean lethal dose-time curves are used to describe the radiation tolerances of 6 species of marine teleosts and 2 species of marine invertebrates. These curves describe radiation tolerances better than the commonly used LD_{50} (30 day) values since they show changes in LD_{50}'s with increasing time after irradiation. In addition, these curves are very useful as guides in experimental design.

Introduction

In our investigations of the effects of sub-lethal doses of radiation on marine organisms, tolerances over wide ranges of dose must be known in order to select levels of radiation that will elicit an effect and still allow a sufficient number of experimental animals to live during the experiment. The tolerance of organisms to ionizing radiation has usually been expressed as the mean lethal dose of radiation 30 days after exposure, i.e. an LD_{50}(30 day). Recent investigations have shown, however, that an LD_{50}(30 day) calculation is insufficient to describe the radiation tolerance of a species because LD_{50}'s vary with time after exposure. In this paper we describe the radiation tolerances of several marine species with mean lethal dose-time curves drawn from dose-time combinations at which 50% of the experimental animals died. The advantages of this manner of presentation over a simple LD_{50}(30 day) are discussed.

Methods

All animals used in these experiments were collected from the Beaufort estuary and were maintained in either standing or flowing estuarine water which was aerated continuously. Water temperature varied less than ± 2°C during an experiment.

Animals were held in the laboratory for five days prior to irradiation to insure the use of only healthy individuals and then were separated into a control group and five or six irradiated groups. Each irradiated group was exposed to one dose in a progressive series of acute radiation doses in a 1,500 curie cobalt 60 irradiator with a 12 x 6 x 6 inch chamber. Because of the large chamber size it was possible to irradiate the animals in groups and thereby minimize individual dose variation. The dose rate in the chamber, measured with glass rod dosimeters, was 480 roentgens (R) per minute ± 10%.

The number of animals which died in each group was recorded daily and LD_{50} values at different times after irradiation were estimated from these data by the method of Reed and Muench (1938). This method was selected because it compensates for both control mortality and the variance in radiation tolerance between individual animals of the same species. By using this method it also was possible to extrapolate certain LD_{50} values for levels of radiation higher than any used in the experiments.

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[1] This investigation was supported through a cooperative agreement between the Bureau of Commercial Fisheries and the U. S. Atomic Energy Commission.

Comparison of Mean Lethal Dose-Time Relations and LD_{50}(30 Day) Values as Expressions of Radiation Tolerance

Initially we used LD_{50}(30 day) values as an index of radiation tolerance but we questioned this practice when radiation doses based on these values killed an unusually large number of animals in experiments lasting 40 or 50 days. Mortality data from the daily records also demonstrated differences in radiation tolerances between species whose LD_{50}(30 day) values were approximately the same. For example, LD_{50}(30 day) values for the mud snail, *Nassarius obsoletus,* (37,500 R) and the sea urchin, *Arbacia punctulata,* (38,900 R) indicated similar tolerances to radiation. Between 30 and 40 days, however, the mortality of sea urchins was greater than that of mud snails and, when LD_{50}'s were calculated at 40 days, the mud snail was twice as resistant to radiation as the sea urchin. We decided, therefore, to calculate LD_{50} values for each species at several different intervals of time after irradiation and to plot these as a mean lethal dose-time curve to obtain a more complete description of species radiation tolerance.

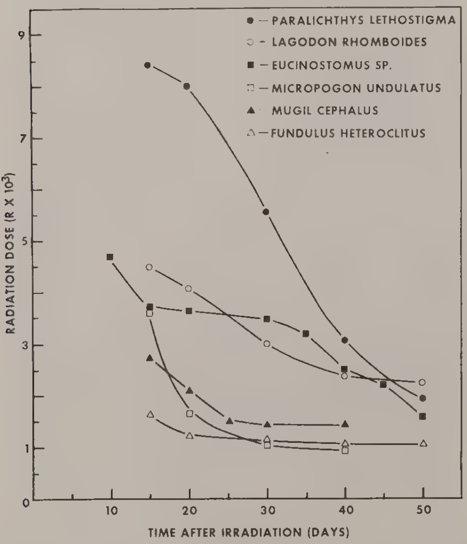

Fig. 1. Mean lethal dose-time curves for several species of marine vertebrates showing the dose-time combinations at which 50% of the experimental animals died.

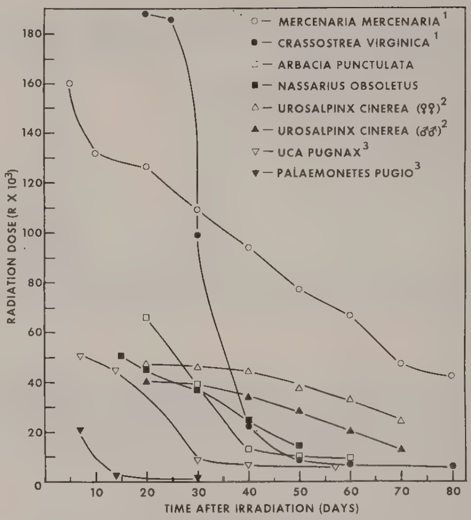

Fig. 2. Mean lethal dose-time curves for several species of marine invertebrates showing the dose-time combinations at which 50% of the experimental animals died. (1) Modified from Price, 1965. (2) Modified from Hargis, et al., 1957. (3) Modified from Rees, 1962.

Graphs of mean lethal dose-time values describe radiation tolerances better than do LD_{50}(30 day) values since they show changes in LD_{50}'s with increasing time after irradiation (Fig. 1 & 2). In general, LD_{50} values decreased with an increase in time after irradiation but the rate of decrease was found to vary both between species and between intervals of time for a single species. These data indicate that LD_{50}(30 day) values do not reflect relative radiation tolerances at other times after irradiation.

LD_{50}(30 day) values obtained for six species of marine teleosts ranged from 1,050 R to 5,550 R (Table 1). Using this index of tolerance, the Atlantic croaker, *Micropogon undulatus*, mummichog, *Fundulus heteroclitus*, and striped mullet, *Mugil cephalus*, were the most sensitive to radiation, whereas the southern flounder, *Paralichthys lethostigma*, was the most resistant. LD_{50}(30 day) values for the mojarra,

TABLE 1. The age, number, and size range of experimental animals and temperatures at which LD_{50}'s were obtained.

Organism	Number of animals	Size (mm S L)	Temp. (°C)	LD_{50} (R) for selected intervals of time — Days after irradiation: 15	20	30	40	50
VERTEBRATES								
Juvenile mummichog *Fundulus heteroclitus*	200	40–50	21	1,650	1,220	1,120	1,075	1,075
Juvenile striped mullet *Mugil cephalus*	105	30–35	18	2,750	2,110	1,450	1,450	—
Postlarval mojarra *Eucinostomus* sp.	385	10–12	22	3,750	3,650	3,500	2,500	1,575
Postlarval pinfish *Lagodon rhomboides*	120	13–17	18	4,500	4,075	3,000	2,375	2,250
Postlarval Atlantic croaker *Micropogon undulatus*	150	15–20	18	3,625	1,650	1,050	925	—
Postlarval southern flounder *Paralichthys lethostigma*	105	8–13	14	8,400	8,000	5,550	3,075	1,925
INVERTEBRATES								
Adult mud snail *Nassarius obsoletus*	105	—	18	51,500	45,500	37,500	24,000	14,000
Adult sea urchin *Arbacia punctulata*	105	—	23	—	66,000 (extrapolated)	38,900	12,500	10,000

Eucinostomus sp., and the pinfish, *Lagodon rhomboides*, were in the middle of the range of radiation tolerances exhibited by the teleosts tested. There are no published LD_{50}'s for marine or brackish water teleosts with which to compare these results, but they are similar to the 1,500 R reported for adult rainbow trout, *Salmo gairdnerii*, (Welander, et al., 1949), and to the 2,315 R (Shechmeister, et al., 1962) and 3,500 rads (Bonet-Maury, 1963) reported for adult goldfish, *Carassius auratus*.

The two marine invertebrates examined, the sea urchin and the mud snail, were approximately seven times more resistant to radiation after 30 days than the most resistant fish (Table 1). The LD_{50}(30 day) value obtained for the mud snail (37,500 R) was higher than the estimate by Bonham and Palumbo (1951) for the marine snail, *Thais lamellosa*, (ca. 20,000 R), but similar to the value for the male oyster drill, *Urosalpinx cinerea*, (38,000 R) estimated from the data of Hargis, et al. (1957).

The LD_{50}(30 day) values obtained from these experiments will be useful for long-term investigations of sub-lethal radiation effects with only the three species of fish whose LD_{50} values changed very little after 30 days: the mummichog, the Atlantic croaker, and the striped mullet (Fig. 1). For these three species, doses near the LD_{50}(30 day) values could be used in experiments longer than 30 days with the assurance that approximately half of the animals would survive. In contrast, the pinfish and the southern flounder showed a high mortality from radiation after 30 days as indicated by the large decrease in LD_{50} values. The mojarra data showed an exception to the type curve most frequently found with two periods of high mortality reflected by decreasing LD_{50}'s. These occurred at 10–15 days and 30–50 days, and possibly indicated radiation damage to two different physiological systems.

The importance of using mean lethal dose-time curves instead of LD_{50}(30 day) values also can be demonstrated with data on marine invertebrates. Price (1965) reported that 93,328 R caused 50% mortality of oysters, *Crassostrea virginica*, in 34 days, and of clams, *Mercenaria mercenaria*, in 38.5 days, indicating similar tolerances to radiation for the two species. Using the Reed and Muench (1938) method with Price's original data (permission by personal communication), it was found that, although the mean lethal doses were similar at about 30 days, the overall radiation tolerances for the two groups of animals were not (Fig. 2). For the first 25 days after exposure the oyster was much more resistant to radiation than the clam, but from 25–50 days after irradiation the oyster had a high mortality. The clam had a lower but comparatively uniform mortality after exposure and the LD_{50} values continued to decrease until after 70 days. After 80 days, the LD_{50} for the clam was greater than for the oyster, a reversal of the tolerances shown at 25 days. The variations in relative LD_{50}'s with time for other marine invertebrates also demonstrate the difficulties of using LD_{50}-(30 day) values as indices of species radiation tolerance (Fig. 2).

The described method of estimating mean species tolerance to radiation by using mean lethal dose-time relations is different from any we have observed and offers several advantages. The present method allows an investigator to choose the dose-time combination best suited to his experiment. We try to select experimental doses of radiation from that portion of the curve where the LD_{50} is independent of time. In doing so we avoid the use of doses which might cause excessively high mortality during an experiment. In addition to their use as guides to experimental design, these curves can be used to compare radiation tolerances between species irradiated under similar conditions.

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NEW RECORDS OF CADULUS (SCAPHOPODA) FROM THE NEW ENGLAND AREA

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Woods Hole, Massachusetts

Two species of small scaphopod mollusks were obtained from benthic fauna collections taken by the U. S. Bureau of Commercial Fisheries in offshore New England waters during the past few years. One species, *Cadulus (Platyschides) rushi rushi* Pilsbry and Sharp, 1898, occurred in samples from the Gulf of Maine. The other species, tentatively identified as *Cadulus (Platyschides) agassizi* Dall, 1881, occurred in samples from moderately shallow water along the southern side of Georges Bank. Some doubt concerning the identity of those specimens tentatively identified as *C. agassizi* results from their slightly longer length and proportionately greater width than is typical for the species (Dr. W. K. Emerson, personal communication).

These records are noteworthy because (1) the genus *Cadulus* has not heretofore been reported from the Gulf of Maine; (2) *C. r. rushi* has not previously been found in such shallow water or as far north; and (3) *C. agassizi* is a southern form that has not been reported from the New England region.

I wish to thank Dr. Joseph Rosewater, U. S. National Museum, and Dr. William K. Emerson, American Museum of Natural History, for identifying these specimens.

CADULUS R. RUSHI

Twenty-four specimens of *C. r. rushi* were obtained at 11 localities in the north-central section of the Gulf of Maine (Fig. 1) by the research vessel *Delaware* on cruise number 61-10, June 23-29, 1961. Collecting devices were a Smith-McIntyre grab sampler and a naturalist's dredge. Shell length of undamaged specimens ranged between 11 and 13 mm. Eleven specimens were alive at the time of capture. Occurrence records and associated data are listed in Table 1. At the localities where these specimens were taken, the water depths ranged from 210 to 256 m. and the bottom sediment at every station was predominantly a mixture of silt and clay of olive-brown color.

A good indication that *C. r. rushi* is restricted to the deeper portions of the Gulf of Maine was its absence in collections from shallow water. No specimens of this species (or genus) occurred in 86 other samples (76 localities) taken on the same cruise at sampling stations spaced 16 km. apart over the northern half of the Gulf. These collections included 23 samples from depths less than 210 m. A deep-water habitat is not unexpected, since the previously established minimum depth for this species was 361 m. (Johnson, 1934). The bathymetric range for *C. r. rushi,* as presently known, is from 210 to 2,811 m. These figures are from Gulf

Table 1.--Collection and specimen data for *Cadulus r. rushi* from research vessel *Delaware* Cruise 61-10, in the Gulf of Maine, June 23-29, 1961 [1]

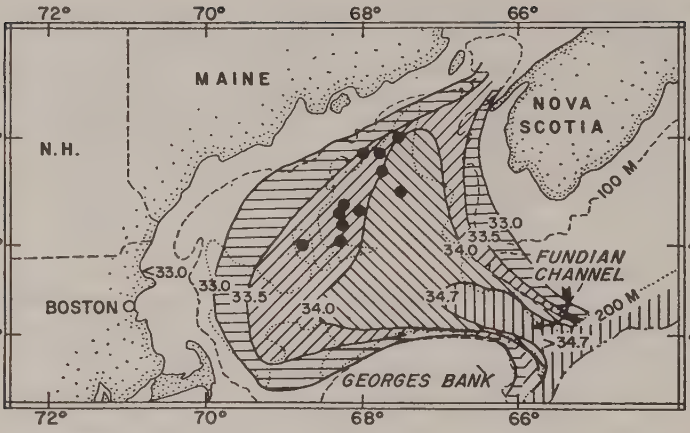
Station number	Location		Water depth (m)	Bottom water temperature (C)	*C. r. rushi* [2]	
	Latitude (North)	Longitude (West)			Number	Length (mm)
26	43°01'	68°45'	220	5.3	2	13, (9-1/2)
55	43°20'	68°01'	247	6.6	1	11
56	43°20'	68°15'	229	6.1	3	13, (5), (2-1/2)
73	43°30'	67°21'	238	6.5	1	(4)
83	43°41	67°46'	238	6.6	1	(5)
91	43°50'	68°00'	210	6.1	1	(9)
92	43°50'	67°45'	256	6.4	5	(9), (6), (6), (2-1/2), (1-1/2)
101	44°00'	67°30'	242	6.1	3	13, 12, (4)
108	43°20'	68°17'	216	6.7	2	12, (4)
109	43°10'	68°17'	234	5.6	3	12, (7-1/2), (4)
110	43°00'	68°15'	210	5.0	2	13, (10)

1/--Bottom sediments at all stations are olive-brown mixture of silt and clay.

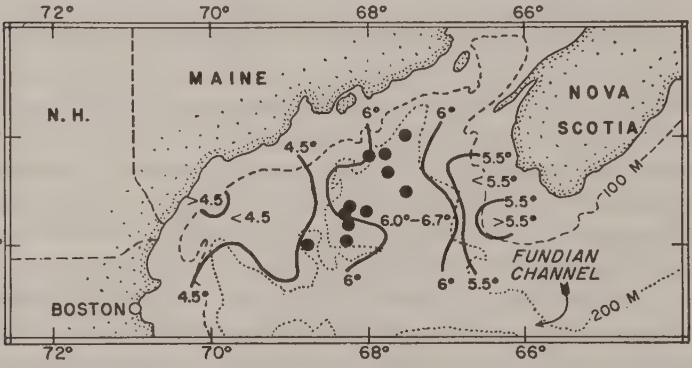
2/--Lengths of incomplete shells are enclosed in parentheses.

of Maine data listed in Table 1, and the maximum depth reported by Henderson (1920) and Clarke (1962).

The geographic range of *C. r. rushi,* as reported by Johnson (1934), extends from Cape Hatteras northward to the vicinity of Georges Bank. Thus its occurrence in the Gulf of Maine — where so far as known it is the only *Cadulus* present — is farther northward than would generally be expected, due to the prominent zoogeographic boundary formed by Cape Cod and Georges Bank. A feature of Gulf of Maine hydrography provides, however, a reasonable explanation why a mollusk from the continental shelf and slope along the eastern coast of the United States could also inhabit certain sections of the Gulf. Bottom water in the deep portions of the Gulf where *C. r. rushi* occurs has a higher salinity than shallower parts. This high-salinity bottom water enters the Gulf through the Funidan (Eastern) Channel (Bigelow, 1927). It spreads northward and westward into the deepest portions of the Gulf (Fig. 1), producing an environment somewhat similar to that on the shelf and slope outside the Gulf. Although salinity measurements were not made at the time these samples were collected, the seasonal and year-to-year changes in bottom-water salinity in the central Gulf are small. The salinity


72°
70°
68°
66°
MAINE
N.H.
NOVA SCOTIA
44°
43°
42°
BOSTON
100 M
200 M
33.0
33.5
34.0
34.7
>34.7
FUNDIAN CHANNEL
GEORGES BANK

1. Geographic distribution of *Cadulus r. rushi* in the Gulf of Maine, and the salinity of bottom water. The salinity data were collected August-September 1964.


72°
70°
68°
66°
MAINE
N.H.
NOVA SCOTIA
44°
43°
BOSTON
100 M
200 M
4.5°
>4.5
<4.5
6°
6.0°-6.7°
5.5°
<5.5°
>5.5°
FUNDIAN CHANNEL

2. Geographic distribution of *Cadulus r. rushi* in the Gulf of Maine, and the bottom-water isotherms (C), June 1961.

gradient of bottom water illustrated in Figure 1 is based on data collected September 1964 aboard the R/V *Albatross IV* (data provided by J. B. Colton, personal communication). On the basis of the information now available, the minimum salinity of Gulf of Maine waters inhabited by *C. r. rushi* appears to be near 33.5°/00.

The high-salinity bottom water that enters the Gulf of Maine through Fundian Channel also has a higher temperature than other Gulf bottom water. At the stations where *C. r. rushi* occurred the bottom temperature at the time the scaphopods were collected ranged from 5.0 to 6.7 C (41-44 F). The distribution of this species in relation to bottom-water temperature in June 1961 is illustrated in Fig. 2. Low water temperature does not appear to be a major deterrent factor in the geographic distribution of this species in the Gulf of Maine, inasmuch as Henderson (1920) has reported its occurrence in slope waters south of the Gulf of Maine at a temperature as low as 2.7 C (36.9 F). The temperature of bottom water in the central Gulf of Maine is rarely less than 4 C (39.2 F). High temperature, however, may be limiting because the Gulf bottom water in some sectors occasionally rises to 8 C (46.4 F). This value is slightly higher than the maximum water temperature (6.6 C or 44 F) associated with *C. r. rushi* as reported by Henderson (1920).

Shell fragility is indicated by the high percentage of broken shells — 16 of 24. The habitat, which consisted of fine-textured sediments in deep-water areas where water currents are generally weak, would not be expected to handicap seriously a thin-shelled species.

CADULUS AGASSIZI

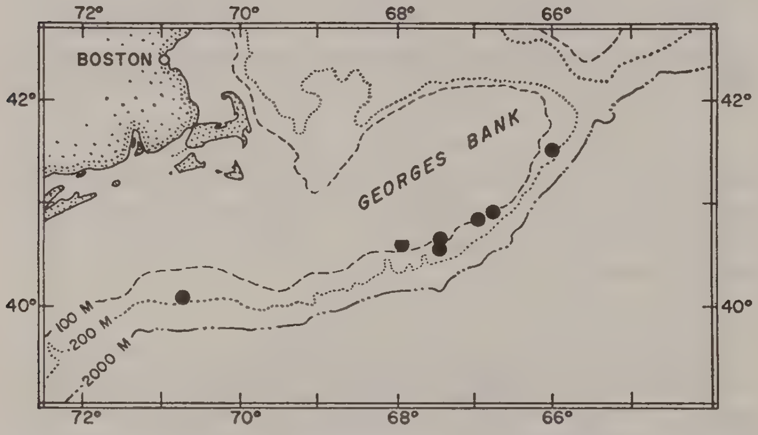
A total of 10 specimens of *C. agassizi* were collected at six stations along the southern periphery of Georges Bank and at one station south of Martha's Vineyard near the edge of the continental shelf. Four of these specimens were collected with a Smith-McIntyre grab sampler, 4 with a trawl, and 2 with a scallop dredge. Shell lengths of the smallest and largest specimens were 7½ and 11 mm. Six of the specimens were alive at capture. The collection data together with the number and size of specimens are listed in Table 2; localities of collection are shown in Fig. 3.

The geographic range for this species has previously been reported as extending from the Florida Keys northward to the Chesapeake Bay region (Johnson, 1934). Thus its occurrence on Georges Bank extends its known range a considerable distance northward and eastward.

Sediments at localities in the Georges Bank region where *C. agassizi* was found were of moderately coarse texture, ranging

Table 2.--Collection and specimen data for *Cadulus agassizi* from the Georges Bank region, 1955-61

Location		Water depth (m)	Date collected	Bottom sediment	*C. agassizi*	
Latitude (North)	Longitude (West)				Number	Length (mm)
40°35'	67°59'	84	November 17, 1955	Gravelly sand	1	10
40°37'	67°28'	86	August 24, 1957	Coarse sand	1	9-1/2
40°50'	66°58'	91	November 19, 1955	Fine sand and shell	3	11, 9, 8-1/2
40°54'	66°46'	102	August 28, 1957	Fine sand and shell	1	9-1/2
40°33'	67°28'	117	August 24, 1957	Medium sand	1	8
41°30'	66°00'	145	August 26, 1957	Gravelly sand	1	8
40°02'	70°47'	146	January 26, 1961	---	2	9, 7-1/2



3. Geographic distribution of *Cadulus agassizi* in the Georges Bank region.

from mixtures of fine sand with shell fragments to sandy gravels. This finding agrees well with sediment types at points of collections of *C. agassizi* reported by Henderson (1920) off the southeast coast of the United States. A large proportion of the collections he cited were from sand substrates or mixtures of sand with shell or rock.

This species has been reported from depths of 31 to 538 m. (Johnson, 1934), and most of the records are from depths between 91 and 274 m. (Henderson, 1920). It was collected from the Georges Bank region at depths between 84 and 146 m., well within the known depth range for the species.

The absence of broken shells of this species suggests that their shells are more durable than those of *C. r. rushi*. This condition would be advantageous for a species such as *C. agassizi* which lives in coarse-textured sediments and at moderate water depths, where water currents are likely to be stronger than in areas of sediment deposition.

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TWO NEW MARINE AMPHIPODS FROM MASSACHUSETTS, U.S.A.

BY

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Specimens of two undescribed species of gammaridean amphipods were found in collections of macrobenthic organisms taken in shallow waters of southeastern Massachusetts and Connecticut. Material was examined from collections made in Great Harbor, Woods Hole; the vicinity of Hadley's Harbor, near Woods Hole; Lake Tashmoo, a small saltwater embayment of Vineyard Sound in Martha's Vineyard Island, Massachusetts; Great Neck Beach, Wareham, Massachusetts; and Mystic River estuary, Mystic, Connecticut. The first species herein described, a member of the genus *Microprotopus,* family Photidae, was found at all Massachusetts localities mentioned above. The second species, a member of the genus *Listriella,* family Liljeborgiidae, was found only in Lake Tashmoo, Martha's Vineyard; Great Harbor, Woods Hole; and Mystic River estuary, Connecticut. Both species are rather small benthic forms, body length 5 mm or less, and both belong to genera containing moderately few species. This is the third species of *Microprotopus* and the ninth species of *Listriella.*

I am grateful to Charles L. Wheeler, Roger B. Theroux, and Timothy W. Robbins for their assistance in collecting specimens, and to Frank A. Bailey for inking figures 1 and 7. I wish to thank Dr. Pierre Brunel, Station de Biologie marine, Grande-Rivière, Canada, for loaning two amphipod specimens collected in Connecticut waters. Also, I am indebted to Dr. E. L. Bousfield, National Museum of Canada, Ottawa, Canada, and Dr. Robert H. Parker, Marine Biological Laboratory, Woods Hole, Massachusetts, for permitting me to examine specimens in their collections.

Microprotopus Norman, 1866

For a diagnosis of this genus, and of the family Photidae to which it belongs, see Stebbing, 1906.

Existing literature contains descriptions of 4 amphipod species that can be considered members of the genus *Microprotopus. M. longimanus* Chevreux and *M. maculatus* Norman occur in European waters and both have been fully and accurately described. However, the remaining 2 species, *M. emissitius* (Dana) from the Sooloo (= Sulu) Sea, Philippines, and *M. hirsuticornis* (Dana) from the Bay of Rio Janeiro (= Rio de Janeiro, Brazil), are insufficiently described for reliable recognition. This genus has not previously been reported from the western North Atlantic Ocean. So far as known, all members of this genus are small benthic forms that inhabit coastal waters less than 22 meters deep.

Microprotopus raneyi [1]) new species (figs. 1-4)

Material examined. — Holotype, adult female, 2.2 mm in length (U.S. National Museum No. 111213), and 1 paratype, female, 2.1 mm in length, collected April 5, 1962, at Lake Tashmoo, an arm of Vineyard Sound, near the village of Vineyard Haven on Martha's Vineyard, Massachusetts. Water depth 2 to 3 m, water temperature 5.5° C, and sediment a silty sand with a few stones and small patches of *Zostera* and algae. Allotype, an adult male, 2.2 mm in length (U.S. National Museum No. 111214) plus 1 male, 1.9 mm in length, and 6 females with lengths of 1.8, 2.0, 2.1, 2.2, 2.2, and 2.7 mm, collected September 12, 1962, in Great Harbor, Woods Hole. Water depth 3 to 5 m, water temperature 18° C, sediment a silty sand. November 13, 1962, the following were collected in Lake Tashmoo, Martha's Vineyard: males 0.9, 1.5, 2.0, 2.0, 2.0, 2.2 mm in length; females 1.3, 1.5, 1.5, 1.6, 2.2 mm in length. Water depth 2 to 3 m, water temperature 9.7° C, sediment primarily silty sand with some gravel and small patches of *Zostera.* Specimens listed above which are not deposited in the National Museum at Washington, D. C., are in the collection at the Bureau of Commercial Fisheries Biological Laboratory, Woods Hole.

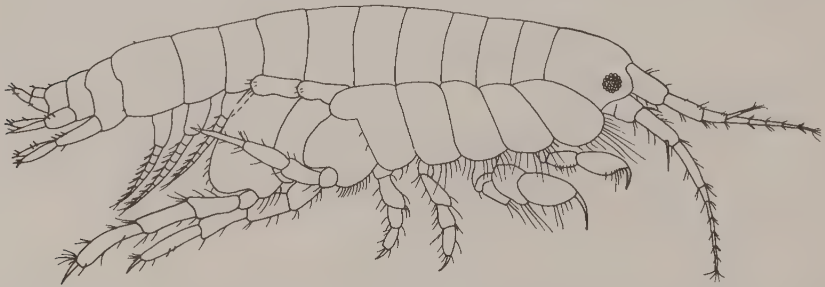

Fig. 1. *Microprotopus raneyi* new species, female, 2.2 mm body length, from Lake Tashmoo, Vineyard Sound, Massachusetts.

Five male specimens having approximate body length of 1.8, 1.8, 1.9, 2.0, 2.0 mm, were collected by Robert H. Parker on August 18, 1964, at Station P-134-64 in the vicinity of Hadley's Harbor, Naushon Island (near Woods Hole), Massachusetts. Water depth at this locality 1 meter, water temperature 20.5° C, salinity 32.02‰, sediment sand. Also in the Hadley's Harbor area, Robert H. Parker collected 1 male approximately 3 mm in length, and 1 female about 2.2 mm in length at Station P-68-64 on February 25, 1964. Water depth 1 meter, water temperature 0.3° C, salinity $32.17^0/_{00}$, substrate gravelly sand.

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[1]) This species is named in honor of Professor Edward C. Raney, Cornell University, Ithaca, New York.

Three specimens, 1 male and 2 ovigerous females, ranging in length from 2 to 3 mm, were collected by E. L. Bousfield on September 12, 1964, at Great Neck Beach, Wareham, Massachusetts. The specimens were taken on an intertidal sand beach, just above the water line at low tide.

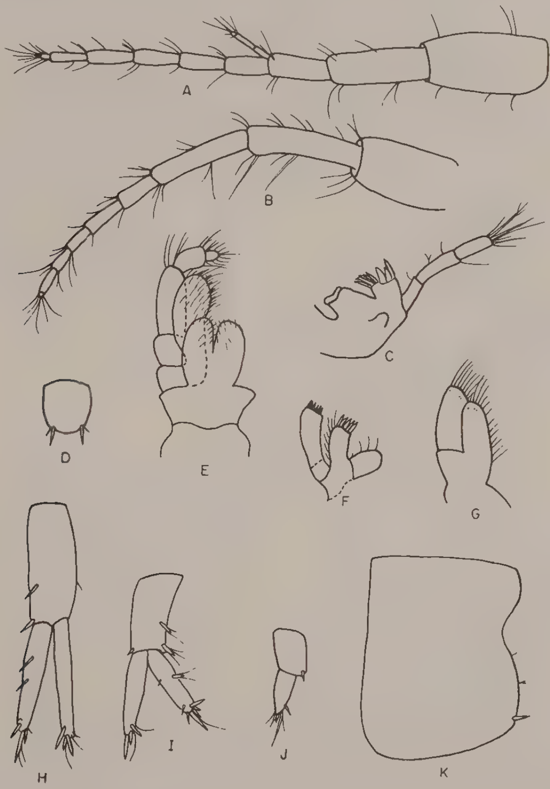

Fig. 2. *Microprotopus raneyi* new species, female, 2.2 mm body length, from Lake Tashmoo, Vineyard Sound, Massachusetts. A, antenna 1; B, antenna 2; C, mandible; D, telson; E, maxilliped; F, maxilla 1; G, maxilla 2; H, uropod 1; I, uropod 2; J, uropod 3; K, third epimeron of pleon.

Female (figs. 1, 2, and 3). — Body length 2.2 mm, moderately stout with medium to small appendages. Head slightly longer than first two pereonites, having the anterior lateral margin produced in short, rounded lobe; rostrum absent.

Eyes distinct, medium-sized, round, composed of about 25 ommatidea. Coxal plates 1 to 4 approximately 1.5 times deeper than broad, ventral margins and inner surfaces setose, first pair expanded distally with minute notch on anterior margin. Coxal plate 5 ventral lobe deep, rounded, lower margin bearing a few short setae; posterior lobe much smaller, also rounded. Coxal plates 6 and 7 shallow, slightly bilobed, posterior lobes bearing short setae. Posterior margin of third pleonal epimeron broadly notched, margin ventral to notch slightly convex, and ventral corner subquadrate bearing a small spine. Pleonites 2 through 6 on some specimens having a few setules on dorsal and dorso-lateral surfaces, most numerous on pleonite 3.

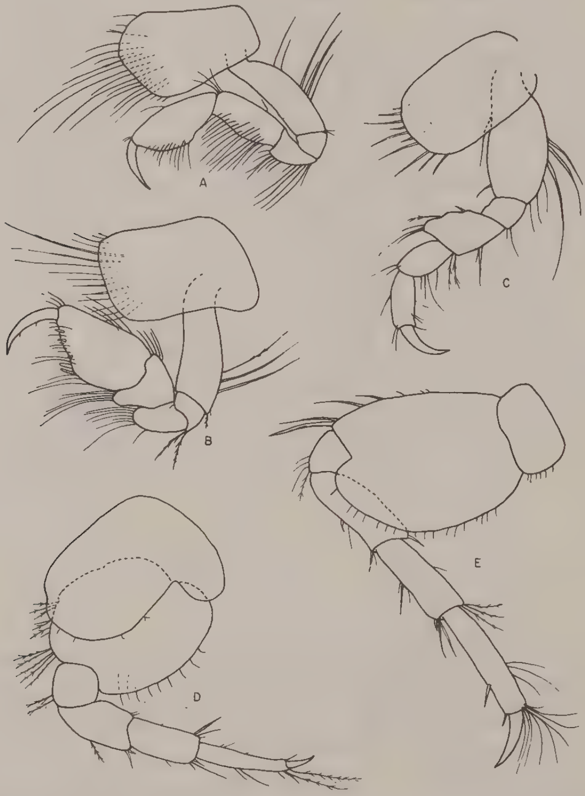

Fig. 3. *Microprotopus raneyi* new species, female 2.2 mm body length, from Lake Tashmoo, Vineyard Sound, Massachusetts. A, pereopod 1; B, pereopod 2: C, pereopod 3; D. pereopod 5; E, pereopod 7.

Antennae 1 and 2 subequal in length, nearly one-third the body length. Antenna 1 peduncle with first article longer and much stouter than the others, article 2 longer and stouter than article 3. Flagellum slightly shorter than peduncle, composed of 5 to 7 articles; accessory flagellum of 2 or 3 articles, shorter than last peduncular article. Antenna 2 peduncle longer than flagellum, third peduncular article stoutest, fourth article longer than fifth. Flagellum of 6 or 7 articles, shorter than flagellum of antenna 1.

Maxillipeds moderately setose, inner plate well developed. Maxilla 1 with 5 stout teeth on inner plate and 6 spines on outer plate. Maxilla 2 with apices and interior margins of both plates setose, apex of inner plate rounded, outer plate apex nearly quadrate. Mandibular palp of 3 articles, article 1 shortest, article 2 longest, article 3 with a number of strong setae at its tip some of which are plumose.

Pereopod 1 moderately large, carpus elongate and setose, propodus expanded with setae most numerous along the palm, dactyl longer than one half the propodus length and with 2 minute spines. Pereopod 2 larger than pereopod 1; carpus deep with ventral linguiform lobe bearing long setae at its distal end; propodus short, broad, densely setose on inner face and with setae and spines on the palm.

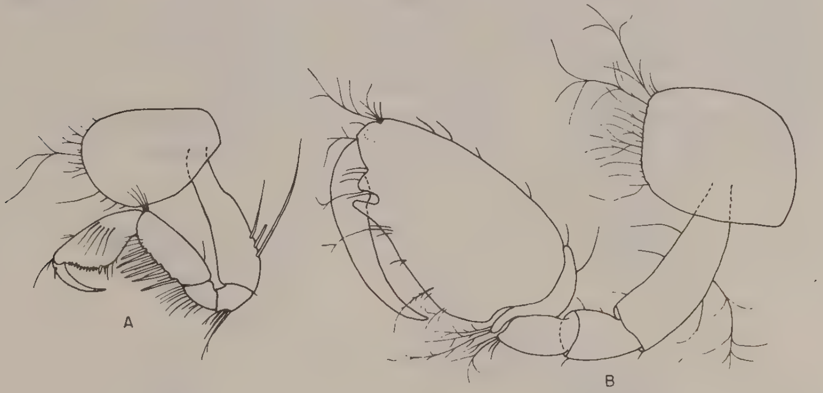

Fig. 4. *Microprotopus raneyi* new species, adult male, 2.1 mm body length, from Great Harbor, Woods Hole, Massachusetts. A, pereopod 1; B, pereopod 2.

Pereopod 3 short; article 2 large; article 3 about one half as long as article 4, expanded anteriorly, lower anterior corner rounded; article 5 broader and slightly shorter than article 6; dactyl large, nearly equal in length to article 6. Pereopod 4 similar to pereopod 3. Pereopod 5 about 1.5 times the length of pereopod 4; article 2 broad, nearly round; dactyl relatively short and stout. Pereopod 6 considerably longer than pereopod 5 and, except for article 2, similar to it in shape; article 2 of pereopod 4 a little shorter and about one third narrower than that of pereopod 5. Pereopod 7 the largest appendage, approximately equal to one half the body length; article 2 large, its width three fourths the length, rounded ventrally; article 3 short; articles 4 and 5 elongate and subequal in length; article 6 nearly 5 times longer than broad; dactyl large.

Uropod 1 biramous, rami and peduncle about equal in length, 2 spines near posterior end of peduncle, apex of each ramus terminating with 3 spines and a few setae. Uropod 2 biramous, shorter and stouter than uropod 1. Uropod 3 uniramous, moderately long but quite stout, ramus equal in length to peduncle, ramus with several apical spines and setae, peduncle with a single posteriorly located spine.

Telson short, somewhat longer than broad, sides nearly parallel, bluntly rounded posteriorly having 1 spine and 1 seta at each corner, very deep in lateral aspect.

Male (fig. 4). — Most external characteristics of the males are morphologically similar to those of the females. The principal differences are the size and shape of the first two pereopods. Pereopods 1 and 2 in males are much larger than in females, particularly pereopod 2 in which, in terminally developed males, the propodus is one fourth the body length. The shape and embellishment of pereopod 2 are also grossly different between the sexes. Males have 2 large teeth at the distal end of the palm, in females the palm is entire. Absence of a tooth on the proximal portion of the ventral margin of the propodus of pereopod 2 is a useful character for distinguishing males of *M. raneyi* from males of *M. longimanus* and *M. maculatus*. This character is reliable even though considerable variation was noted in dactyl length and propodus shape in pereopod 2 of males.

The antennae are proportionally longer in males. The flagellum of antenna 1 consists of 6 to 8 segments, that of antenna 2 has 6 to 7 segments.

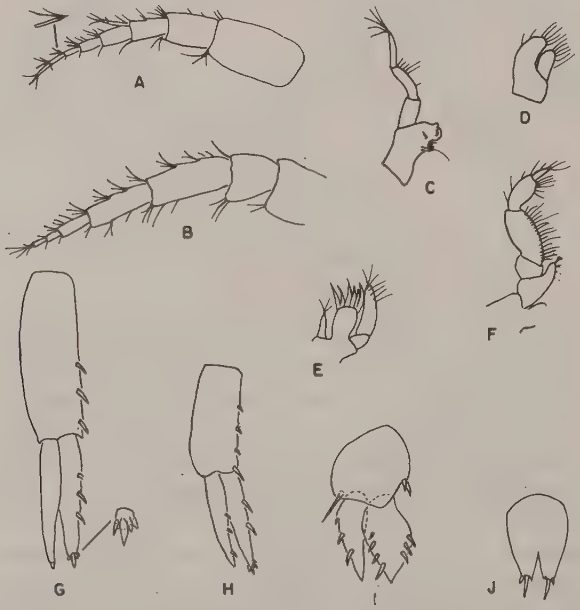

Fig. 5. *Listriella barnardi* new species, male, 4.0 mm body length, from Lake Tashmoo, Vineyard Sound, Massachusetts. A, antenna 1; B, antenna 2; C, mandible; D, maxilla 2; E, maxilla 1; F, maxilliped; G, uropod 1; H, uropod 2; I, uropod 3; J, telson.

The body and appendages are generally more setose in males, this is particularly noticeable on the antennae and pleon dorsum. Plumose setae of a somewhat unusual type, illustrated in fig. 4, are common in males but rarely occur in females.

Color. — Color of living specimens has not been observed. Specimens freshly preserved in formalin appear brown or blackish to the unaided eye, but under magnification the color is dark violet brown. The intensity of pigmentation and the area covered varies considerably from one specimen to another. Some are lightly pigmented; however, usually there is moderately dense pigmentation covering a large portion of the body plus the proximal parts of the larger appendages. Distinct transverse pigment bands, of which there are usually 9, extend across the dorsal body surface and part way down the sides; they are widest and most pronounced on pleonites 1 to 3. Eyes blood-red.

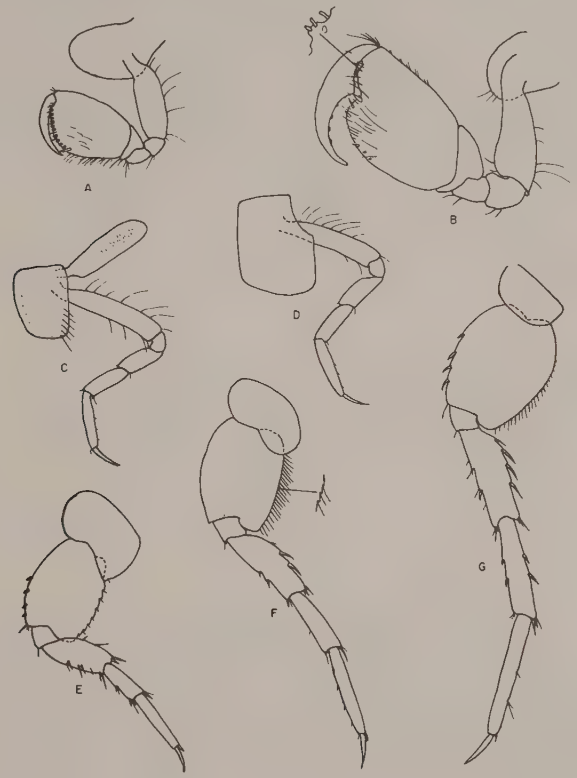

Fig. 6. *Listriella barnardi* new species, male, 4.0 mm body length, from Lake Tashmoo, Vineyard Sound, Massachusetts. A, pereopod 1; B, pereopod 2; C, pereopod 3; D. pereopod 4; E, pereopod 5, F, pereopod 6; G, pereopod 7.

Distribution. — This species is known to occur in Lake Tashmoo (Vineyard Sound), Martha's Vineyard; Great Harbor, Woods Hole; vicinity of Hadley's Harbor near Woods Hole; and Great Neck Beach, Wareham, Massachusetts.

Habitat. — This species is known to occur from the low intertidal to depths of 5 m, based on environmental data from the collection sites listed above. Water temperature extremes at the localities where this species was collected ranged from 0.3° to 20.5° C. These values are within a few degrees of the annual temperature range of shallow waters in this region. The annual range in water salinity at the above localities is estimated to have been approximately 31.0 to $32.5^{0}/_{00}$. The bottom sediments where *M. raneyi* was found include such varied types as gravelly sand, sand, silty sand with occasional stones and patches of *Zostera* and algae.

Other species of amphipods taken in the Lake Tashmoo and in Woods Hole collections with *Microprotopus raneyi* were: *Ampelisca* sp. *A. macrocephala* Liljeborg, *Ampithoe rubricata* (Montagu), *Batea catharinensis* Müller, *Carinogammarus mucronatus* (Say), *Cymadusa filosa* Savigny, *Elasmopus levis* (Smith), *Lembos smithi* (Holmes), *Listriella clymenellae* Mills, *Listriella barnardi* n. sp., *Lysianopsis alba* Holmes, *Microdeutopus damnoniensis* (Bate), and *M. gryllotalpa* Costa. The most abundant of these were *C. mucronatus* and the two species of *Microdeutopus,* which are common shallow-water forms frequently associated with algae or eelgrass.

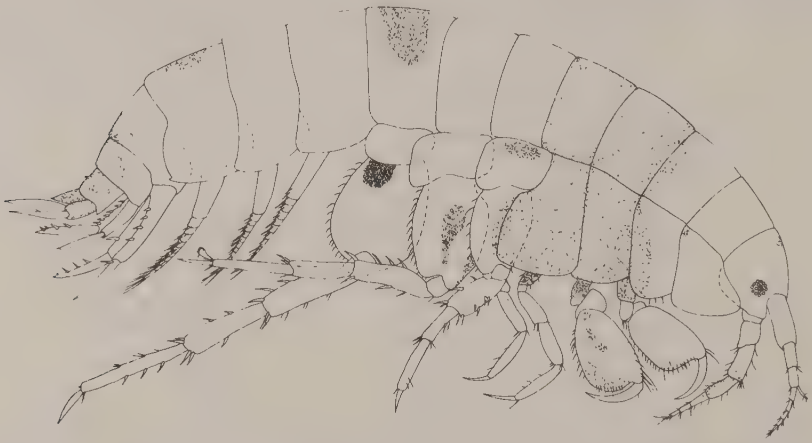

Fig. 7. *Listriella barnardi* new species, female, 4.8 mm body length, from Lake Tashmoo, Vineyard Sound, Massachusetts.

The approximate density of the *M. raneyi* population in Lake Tashmoo can be judged from 10 quantitative samples taken with a $1/10\ m^2$ Van Veen grab sampler. On November 13, 1962, 11 specimens were taken in the 10 samples. The density ranged from 0 to $25/m^2$; the overall average was $11/m^2$.

Remarks. — In the collection made April 5, 1962, in Lake Tashmoo, 6 females were examined that ranged in length from 1.8 to 2.7 mm; 5 were ovigerous, including the three smallest specimens. The numbers of ova in these specimens were 6, 6, 7, 8, and one specimen contained 3 ova but it was obvious that some were missing from this clutch. The ova were spherical to slightly oblong, ranging between 0.2 and 0.3 mm in diameter; the color after preservation in formalin was whitish to semi-transparent.

KEY TO THE SPECIES OF MICROPROTOPUS

1a. Antennae short, one fourth body length; female: pereopod 2 simple, propodus 3 times as long as broad; male: propodus of pereopod 2 with 3 large teeth on palm, proximal tooth largest . . . . *M. longimanus*

b. Antennae comparatively long, one third to one half body length; female: pereopod 2 subchelate, propodus 1.5 to 2 times as long as broad; male: palm of propodus of pereopod 2 with 2 or 3 teeth (if three, middle tooth largest) 2

2a. Third pleonal epimeron with 3 or 4 setae on postero-ventral margin; female: propodus of pereopod 1 moderately broad, propodus of pereopod 2 twice as long as broad; male: palm of propodus of pereopod 2 with 3 teeth (middle tooth largest) . . . . . . *M. maculatus*

b. Third pleonal epimeron with 1 spine and several setae on postero-ventral margin; female: propodus of pereopod 1 slender, propodus of pereopod 2 1.4 to 1.7 times as long as broad; male: palm of propodus of pereopod 2 with 2 teeth . . . . *M. raneyi*

Listriella J. L. Barnard, 1959

Listriella was established by Barnard (1959) in his revision of the family Liljeborgiidae (see for definitions Barnard's paper). At the present time this genus contains 5 species from southern California (Barnard, 1959); 1 from Europe and another from the tropical Pacific, that were formerly placed in the genus *Idunella,* which Barnard transferred to *Listriella.* Further, the genus contains 1 species from Cape Cod, Massachusetts, *L. clymenellae,* recently described by Mills (1962).

Listriella barnardi [2]) new species (figs. 5-8)

Material examined. — Holotype, adult male, 4.0 mm in length (U.S. National Museum No. 111216); allotype, adult female, 3.4 mm in length (U.S. National Museum No. 111215); and 2 paratypes, females with lengths of 2.6 and 3.3 mm; all collected August 5, 1962, in Lake Tashmoo. Additional specimens from Lake Tashmoo collected November 13, 1962, as follows: males, 3.0, 3.5, and 4.0 mm in length; females, 3.0 and 3.5 mm in length. The type specimens have been deposited in the U.S. National Museum, the others are in the collection at the Bureau of Commercial Fisheries Biological Laboratory, Woods Hole. Two specimens were examined from the collection at Station de Biologie marine, Grande-Rivière, Canada. These specimens, one male 5.0 mm in length and one female 3.0 mm in length, were collected by W. G. Pearcy from stomachs of small blackback flounders, *Pseudopleuronectes americanus* (Walbaum), in the Mystic River estuary, Connecticut, on August 11, 1959.

Male. — (figs. 5, 6, and 7). Body length 4.0 mm, stout with rather short appendages, except pereopods 5 to 7 which are moderately long. Head short, length equal to its greatest depth, excavated anteriorly forming a short rostrum. Eyes round, medium to large, composed of approximately 15 ommatidea. Coxal plates 1 to 3 moderately short; 4th coxa longer, upper posterior margin broadly indented, setae sparse; coxal plates 5 to 7 small, broader than deep, plates 5 and 6 somewhat bilobed ventrally. Posterior margin of third pleonal epimeron having a shallow excavation mid-laterally, lower portion convex, and a small notch on posterior ventral corner. Posterior dorsal portions of pleonites 4 and 5 slightly mucronated in some of the larger specimens. Sixth pleonite with a short spine on dorsum.

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[2]) Named for Dr. J. Laurens Barnard, Beaudette Foundation for Biological Research, Moss Landing, California.

Antennae short, about one fifth body length, antenna 1 slightly shorter than antenna 2. Peduncle of antenna 1 moderately stout, especially article 1; flagellum two thirds as long as peduncle, composed of 5 articles, among regular setae a few club-shaped setae (see inset in fig. 5 A); accessory flagellum of 2 articles, distal article much the smaller. Peduncle of antenna 2 moderately stout, article 3 quite short with a pronounced anteroventral lobe; flagellum short, only one third the peduncle length, consisting of 4 articles.

Maxilliped moderately setose, dactyl terminating in a stout spine; outer plate small; inner plate short, broad, sparsely setose. Maxilla 1 palp and inner plate with setose apices, outer plate with six strong, curved dentate spines. Maxilla 2 with few fine setae on both plates, outer plate small. Mandibular palp of three articles, first article stout and elongated, terminal article with several long setae at apex and a linear series of shorter setae near apex; molar process of mandible small.

Pereopod 1 much smaller than pereopod 2, ischium and merus small; carpus deep and narrowed ventrally; propodus expanded and somewhat narrowed proximally, its length about one half the length of propodus of pereopod 2, inner face sparsely setose, occluded margin entire, bearing setae and about 10 to 15 short, uniform, peg-like spines, ventral margin setose; dactyl large, without projection on inner margin. Pereopod 2 nearly twice as large as pereopod 1 and similar to it except for the 2 distal articles. Propodus broad, narrowed proximally, inner face sparsely setose, occluded margin bearing setae and irregular-sized spines, margin indented, with a squared tooth-like projection above indentation; dactyl large having wedge-shaped projection opposite notch in margin of propodus, knobules occurring along occluded margin. Compared to propodus of left pereopod 2, right propodus is considerably broader distally, with fewer setae along dorsal margin and more setae along ventral margin.

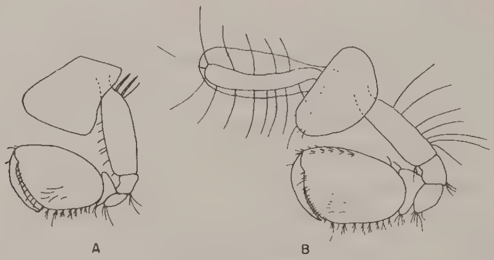

Fig. 8. *Listriella barnardi* new species, female, 4.8 mm body length, from Lake Tashmoo, Vineyard Sound, Massachusetts. A, pereopod 1; B, pereopod 2.

Pereopod 3 slender, sparsely setose; article 2 long, length more than 5 times width; article 3 short, length less than width of article 2; articles 4 and 5 subequal; article 6 narrow; dactyl pointed, half as long as article 6. Pereopod 4 similar to pereopod 3. Pereopods 5 to 7 of progressively larger size, stouter than pereopods 3 and 4, spinose; article 2 somewhat expanded, spines along anterior margin, posterior margin serrulate with setae (see inset of fig. 6 F); article 3 squarish; articles 4 to 6 elongate, each segment successively narrower; dactyl slender, length 2.5 to 3 times width of propodus, pointed.

Uropod 1 spinose, biramous, rami of equal length, apex of inner ramus with cluster of small spines (see inset in fig. 5 G), length of peduncle one and one fourth that of rami. Uropod 2 similar to uropod 1, but smaller and rami equal in length to peduncle. Uropod 3 spinose and biramous; rami of equal length; inner ramus broad, width about one half the length; outer ramus consisting of only one article; peduncle short and broad, width equals length.

Telson longer than peduncle of uropod 3, tapering slightly toward terminal end, cleft extending nearly half its length, one large and one small spine located near posterior apex of each lobe.

Female (fig. 7). — Body length 4.8 mm. Similar to male except for the following major differentiating characteristics: coxal plates 1 to 3 deeper and somewhat narrower; oöstegites narrow with long setae; pereopods 1 and 2 (fig. 8) much smaller, subequal, propodus only about one tenth body length; occluded margin of propodus of pereopod 2 entire, dactyl without tooth-like projection; rami of uropod 3 relatively narrow and elongate.

Color. — The basic color is white with various-sized irregular patches of dark purple on the body and appendages as indicated in fig. 7. The largest pigmented patch is a transverse band which extends completely across the body on pereonites 3 and 4 with some extending on adjacent segments. A moderately wide transverse band crosses pereonite 7. Another rather large patch covers most of the telson and the posterior portion of the pleon. A small spot occurs mid-dorsally on the head; miscellaneous bands and patches occur on the antennae and the basal portions of the pereopods. The pigment tends to fade in preservative; the darkest and most persistent patch occurs on the basal segment of pereopod 7. The eye is scarlet. The pigmentation density is variable from one specimen to another; even the saddle patch on pereonites 3 and 4 is faint on some specimens.

Distribution. — This species is known to occur in Lake Tashmoo, Martha's Vineyard, Massachusetts, and the Mystic River estuary, Connecticut. The Mystic River estuary is located approximately midway between New London and the Connecticut-Rhode Island boundary.

Habitat. — The collecting site in Lake Tashmoo was at depths of 2 to 3 m on a substratum of silty sand containing some gravel and occasional patches of *Zostera* and algae. The general temperature and salinity information is mentioned in the habitat discussion for *Microprotopus raneyi.* Inasmuch as *Listriella clymenellae* is known to live in tubes with *Clymenella torquata* (Leidy) it may be suspected that *L. barnardi* also lives associated with a polychaete. The grab samples containing *L. barnardi* contained numerous species of polychaetes, but the only tubes observed that were large enough for *Listriella* were those of *Clymenella.*

Other species of amphipods that occurred in the same samples with *L. barnardi* were: *Ampelisca* sp., *Jassa falcata* (Montagu), *Listriella clymenellae* Mills, *Microdeutopus damnoniensis* (Bate), *M. gryllotalpa* Costa, and *Microprotopus raneyi* n. sp. The first two of those species were the most abundant.

The density of *L. barnardi* in Lake Tashmoo on November 13, 1962, varied from 0 to 25/m², based on 10 samples taken with a 1/10 m² Van Veen grab. The average density of all samples was 5/m².

Remarks. — One characteristic of this genus is that the outer ramus of uropod 3 consists of two articles, sometimes fused into one article (Barnard, 1959). Adults of both *Listriella barnardi* and *L. clymenellae* have, so far as known, only one article forming the outer ramus of uropod 3. Also, specimens of *L. clymenellae* 1.5 mm in length have only one article forming the ramus. Juveniles of *L. barnardi* are not available for examination. Because of the limited information available on this subject, the apparent non-conformity of *L. clymenellae,* and possibly *L. barnardi,* in this generic character presents insufficient ground for excluding these species from *Listriella.*

RESUMÉ

Descriptions de deux nouveaux Amphipodes marins, *Microprotopus raneyi* et *Listriella barnardi,* capturés au sud-est de l'état de Massachusetts, États Unis de l'Amérique.

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CAPRELLA GRAHAMI, A NEW SPECIES OF CAPRELLID (CRUSTACEA: AMPHIPODA) COMMENSAL WITH STARFISHES

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A new species of caprellid amphipod that lives commensally with starfishes of the family Asteriidae was found in coastal waters of southern New England. The first specimens were detected in collections of marine invertebrates dredged in Vineyard Sound, off Falmouth, Massachusetts, by personnel of the Marine Biological Laboratory. These collections were made in March, 1965; subsequent collections in April and June, 1965, demonstrated that the species occurs in Great Harbor at Woods Hole, the passages between Vineyard Sound and Buzzards Bay, and the Cape Cod Canal. Specimens from Long Island Sound were collected by Clyde L. MacKenzie, Bureau of Commercial Fisheries Biological Laboratory, Milford, Connecticut. The restricted association of these caprellids with starfishes prompted a close examination of this amphipod species.

This appears to be the only known commensal relationship between a caprellid and starfishes in the Western Atlantic region.

We thank John J. Valois and David H. Graham, Marine Biological Laboratory, Woods Hole, for their assistance in obtaining starfish and caprellids used in this study; Thomas E. Bowman and John C. McCain for suggestions for improving the manuscript and bringing to our attention the specimens collected by Clyde L. MacKenzie, Jr., in Long Island Sound; and Frank A. Bailey for inking the drawings.

Caprella grahami [1] new species

Figures 1–5

Diagnosis

Moderately large *Caprella* with head rounded anteriorly; in male, distal segments of peduncle of antenna 1 densely covered with minute setae; body segments without setae, spines, or tubercles; maxillipeds, gnathopods, and pereopods with stout dactyls; propodus of posterior three pairs of pereopods without spines and with only a few setae, palm margin slightly convex to slightly concave.

Descriptions and illustrations of the genus *Caprella* are given by Mayer (1903), Kunkel (1918), and Steinberg and Dougherty (1957).

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[1] Named in honor of Dr. Herbert W. Graham, Laboratory Director, Bureau of Commercial Fisheries Biological Laboratory, Woods Hole, Massachusetts.

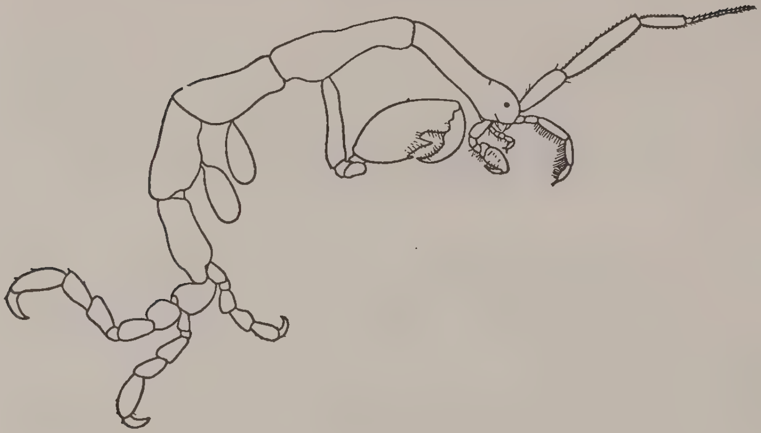

FIGURE 1. *Caprella grahami* new species, lateral view of adult male.

Description of male (Figs. 1–3)

Head elongate, rounded anteriorly, section posterior to groove one to two times as long as anterior section, posterior section shortest in small specimens. Pereods 2–4 slightly inflated ventrally and laterally. Pereods 2–7 smooth, without setae, spines, or tubercles. Cuticle of pereods and appendages, or portions thereof, in some specimens sculptured with small disc-like markings. Pereod 2 longest, equal in length to head; pereods 3 and 4 equal in length, about $\frac{2}{3}$ as long as pereod 2; pereods 5–7 progressively shorter.

Antenna 1 large, nearly $\frac{1}{2}$ body length; peduncle rather stout, distal segments densely covered with small setae; distal peduncular segment with small spine-like projection on anterodorsal margin; distal peduncular segment slightly shorter than basal segment; middle segment twice as long as distal segment; flagellum 9 to

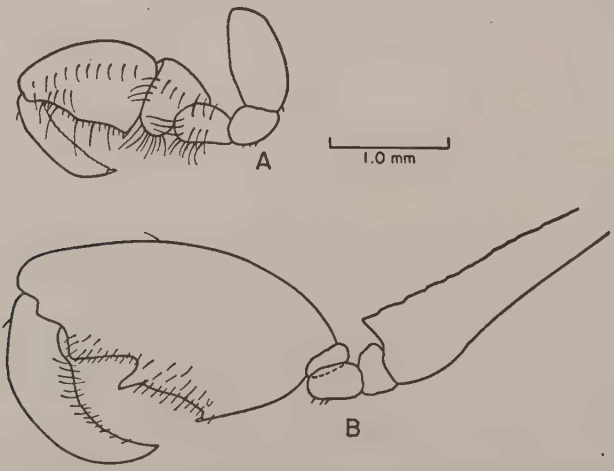

FIGURE 2. *Caprella grahami* new species, adult male (A) gnathopod 1 and (B) gnathopod 2.

14 segmented, flagellum approximately ⅓ total antenna length. Antenna 2, about ½ the length of antenna 1, extending to middle or distal end of second peduncular segment of antenna 1; peduncular segment 1 with lobe-like projection extending

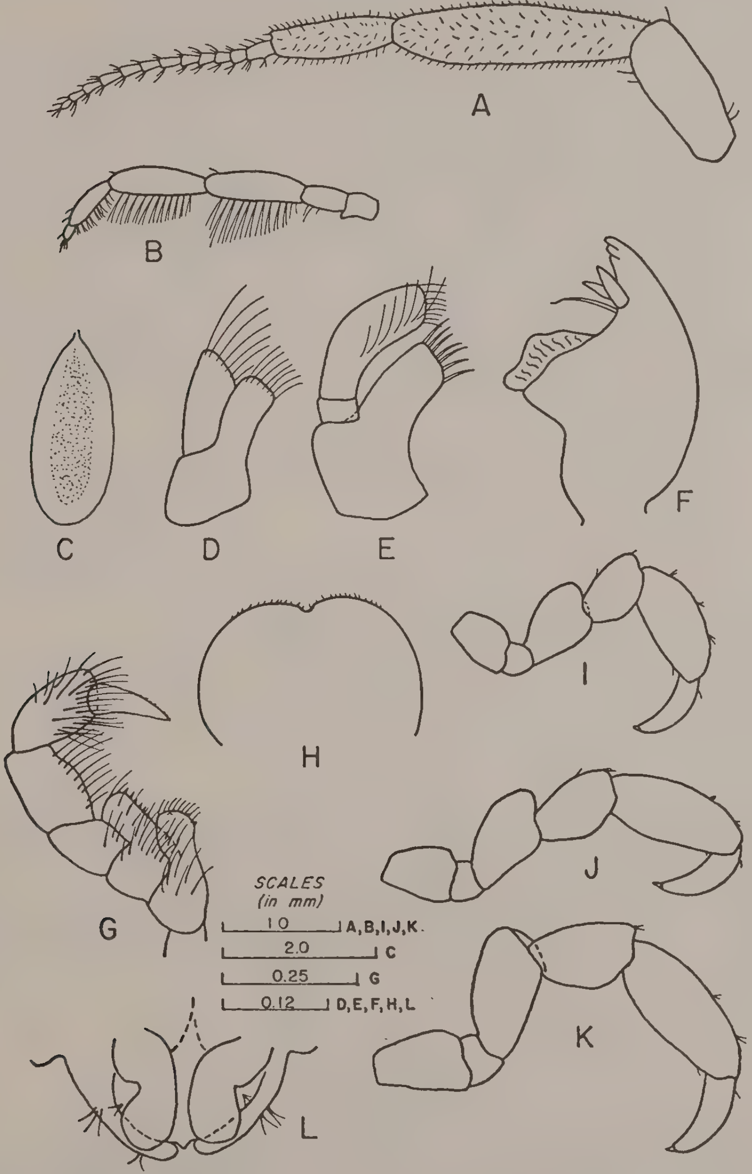

FIGURE 3. *Caprella grahami* new species, adult male (A) antenna 1, (B) antenna 2, (C) gill, (D) maxilla 2, (E) maxilla 1, (F) mandible, (G) maxilliped, (H) upper lip, (I) pereopod of 5th pereod, (J) pereopod of 6th pereod, (K) pereopod of 7th pereod, and (L) pleon.

anteriorly from anteroventral margin; peduncular segments 3–5 with row of long paired setae along ventral margin, longest on segment 3, moderately long on 4, shortest on 5; flagellum consists of a single segment.

Mouthparts typical of the genus. Maxillipeds with stout dactyls; maxilla 1 with longitudinal row of setae on distal segment of palp.

Gnathopod 1 small, subchelate; dactyl relatively large and broad, occluded margin minutely serrate, spine inset at apex; propodus broad (width equals $\frac{2}{3}$ length), setae on inner lateral face, palm margin nearly straight, bearing long and short setae, small spine at proximal end. Gnathopod 2 very large, subchelate; attachment to body located on posterior half of pereod 2; dactyl long and broad, occluded margin entire and setose, outer (anterior) margin on some specimens with tiny knobs. Propodus long and broad (width equals $\frac{1}{2}$ length), configuration of palm margin includes deep sinus midway along palm that separates broad, angular lobe distally from large tooth-like projection ("poison tooth") proximally; at proximal end of palm margin a small spine arises from moderate-sized lobe; broad but shallow excavation with straight margin separates "poison tooth" from proximal spine; small spine on inner face of propodus just above and slightly distal to large proximal spine. Carpus very small, merus and ischium small. Basis medium to long ($\frac{1}{2}$ to $\frac{3}{4}$ propodus length) and narrow (about two to four times maximum width), anterior margin finely irregularly sinuate, distal anterior corner sharply angular.

Gills elliptical to obovate; size moderate, length about equal to or greater than $\frac{1}{2}$ their pereod lengths.

Pereopods on pereods 5, 6, and 7 consist of 6 segments; all segments medium to moderately stout; dactyls broad; propodus large, length about $2\frac{1}{2}$ times maximum width; propodus without spines, and setae exceedingly sparse, palm margin usually slightly concave but sometimes straight or slightly convex.

Pleon minute. Uropod 1 comparatively wide, without setae, apex broadly rounded and entire. Uropod 2 narrow, sparsely setose, apex rounded and entire.

Description of female (*Figs. 4 and 5*)

Females are morphologically similar to males in many features; only the principal differences are mentioned here. Head similar to that of males but much shorter, section posterior to groove approximately equal in length to anterior section. Attachment of gnathopod 2 located on anterior half of pereod 2 (rather than on posterior half as in males). Peduncle of antenna not densely covered with setae. Flagellum consists of 8 to 10 segments. Antenna 2 proportionately longer than in

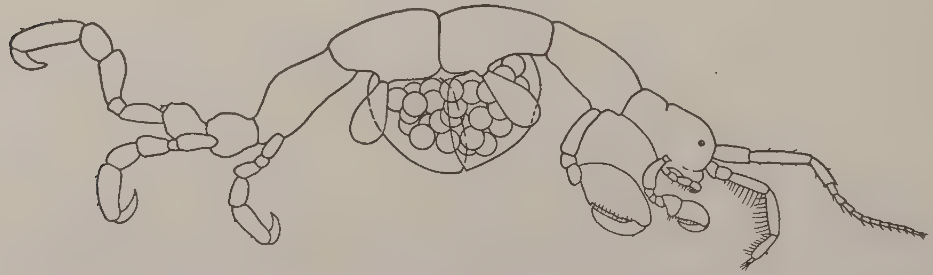

FIGURE 4. *Caprella grahami* new species, lateral view of adult female.

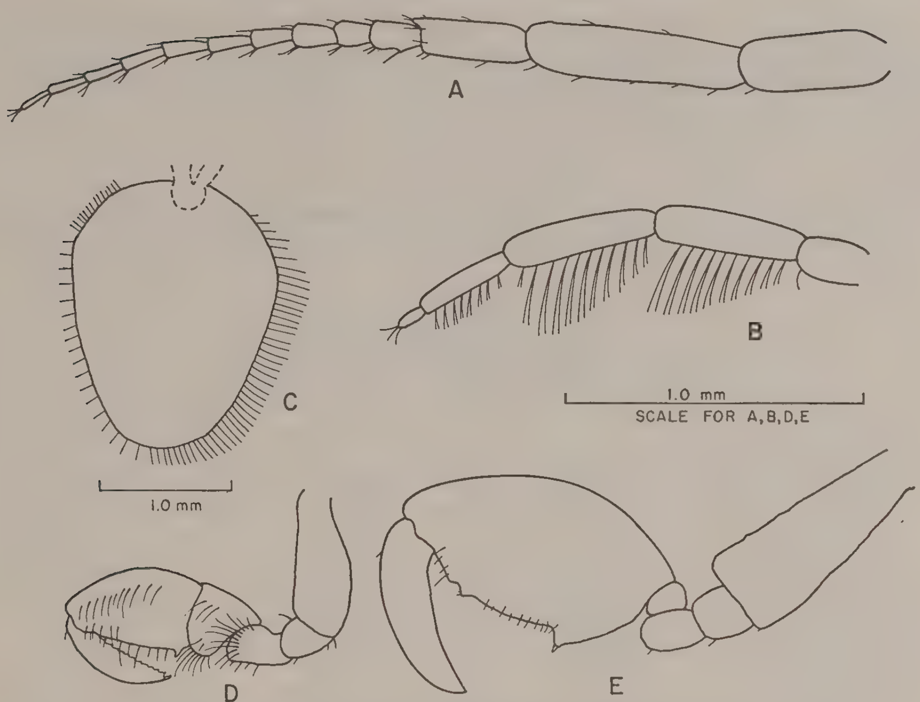

FIGURE 5. *Caprella grahami* new species, adult female (A) antenna 1, (B) antenna 2, (C) oostegite of pereod 3, (D) gnathopod 1, and (E) gnathopod 2.

male, nearly $\frac{3}{4}$ the length of antenna 1 or $\frac{1}{3}$ the total body length. Gnathopods proportionately smaller, particularly gnathopod 2; propodus palm margin of gnathopod 2 convex (without sinus or excavation), with small relatively broad tooth in middle of palm margin, and spine at proximal end. Pereod 2 relatively shorter; pereods 3 and 4 expanded laterally. Oostegites on pereods 3 and 4 large, slightly overlap one another medially and laterally; entire margin, except mid-dorsal section, fringed with setae; oostegite of pereod 3 with marginal setae comparatively long, particularly on posterior margin, and a brush-like group of setae on anterodorsal margin; oostegite of pereod 4 with minute marginal setae.

Shape of ova varied from slightly oblong to spherical. Ova size ranged from 0.38 to 0.46 mm., based on the measurement (maximum length) of 10 ova each from three females. Numbers of ova in three specimens were: 42, 44, and 47.

Juvenile specimens

Proportional sizes of appendages and body segments of juvenile specimens (2 to $3\frac{1}{2}$ mm., body length) differ substantially from those of adults. Antenna 1 incompletely developed, only slightly larger than antenna 2. Flagellum of antenna 1 composed of three segments; flagellum of antenna 2 one-segmented. Head short, posterior section about half as long as anterior section. Pereods relatively very stout, depth of pereod 2 equals its length. Gnathopods proportionately large but lack shape characteristic of adults. Pereopods also proportionately large, reveal some of the most distinctive features that characterize this species. Consequently, pereopods are one of the key components to be examined in identifying juvenile specimens of *C. grahami*.

Size

Body lengths of preserved specimens of *C. grahami* range from 2 to 18 mm. (Table I). Males are larger than females; maximum lengths observed for each are 18 and 8 mm., respectively. Minimum body length for both sexes is 3½ mm. Males generally average between 8 and 12 mm., females average 5 to 7 mm., and juveniles range from 2 to 3½ mm. The development of adult characteristics becomes evident in both sexes at body lengths of 3½ to 4 mm.

TABLE I

Range in body lengths of C. grahami
(Length measured from the anterior margin of head to posterior tip of pleon; number of specimens measured is shown in parentheses)

Date of collection (1965)	Body length (mm.)		
	Males	Females	Juveniles
March 6	5½–11 (8)	4 –6½ (4)	—
March 25	—	–8 (1)	—
March 29	4 – 8½ (6)	3½–7 (12)	2½–3½ (7)
March 30	5½–18 (17)	5 –7½ (17)	2½–3 (3)
April 20	4½–15 (18)	4 –8 (33)	3 –3½ (2)
April 22	3½–10 (4)	4½–6½ (9)	2 –3½ (7)
June 23	3½– 5½ (9)	3½–5 (11)	—
June 24	—	5 (1)	—

Color

Color of body and appendages variable from one specimen to another, ranging from nearly transparent to yellow-orange and red. In the majority of specimens the color is rather uniform light yellow-orange over the entire animal; about 10%, however, have broad transverse bars or patches of red on the body and appendages that contrast sharply with the transparent or light yellowish-orange of the remaining areas. The eye is bright red. In alcohol-preserved specimens the large gnathopods are frequently medium to dark yellow, whereas other parts of the body are light yellow or whitish. Color pattern does not appear to be related to age, sex, locality, or host.

Range

Coastal waters of southeastern New England, U. S. A.; Long Island Sound, Vineyard Sound, Great Harbor in Woods Hole, passages between Vineyard Sound and Buzzards Bay, Cape Cod Canal; in water depths of 0.3 to 25 m. Has been found only in marine waters of full salinity (about 32‰).

Material examined

Holotype, adult male 15 mm. long, deposited in the U. S. National Museum (No. 113031). Allotype, ovigerous female 7 mm. long (USNM No. 113032). Paratypes, 17 males ranging in length from 4½ to 14 mm.; 32 females ranging in length from 4 to 8 mm.; and two juveniles 3 and 3½ mm. long. All type specimens were taken from a single *Asterias forbesi,* 7½ cm. radius. Collection was made April 20, 1965, at water depths of 10 to 15 m. in Vineyard Sound, 3 km. northeast of Nobska Point, off Falmouth, Massachusetts. Specimens were collected by John J. Valois and Paul Shave.

Quicks Hole (between Buzzards Bay and Vineyard Sound); water depth 8 m.; water temperature 3.9° C.; March 29, 1965; 35 specimens (6 males; 12 females, 7 ovigerous; 7 juveniles) on *Asterias forbesi.*

Quicks Hole; water depth 8 m.; water temperature 6.1° C.; April 22, 1965; 20 specimens (4 males; 9 females, 5 ovigerous; 7 juveniles) on *Asterias forbesi* and *Asterias vulgaris.*

Lagoon Pond, Martha's Vineyard (Vineyard Sound); water depth 0.3 to 2 m.; June 23, 1965; 20 specimens (9 males; 11 females, 10 ovigerous) on *Asterias forbesi.*

Great Harbor in Woods Hole; water depth 13 to 20 m.; water temperature 3.9° C.; March 25, 1965; one female on *Asterias forbesi.*

Vineyard Sound, 3 km. south-southeast of Nobska Point; water depth 22 to 25 m.; March 30, 1965; 37 specimens (17 males; 17 females, 16 ovigerous; 3 juveniles) on *Asterias forbesi.*

Vineyard Sound, 3 km. northeast of Nobska Point; water depth 9 m.; water temperature 3.4° C.; March 6, 1965; 12 specimens (8 males; 4 females, 2 ovigerous) on *Asterias forbesi.*

Cape Cod Canal, Sandwich; water depth 1 m.; June 24, 1965; one ovigerous female; on *Asterias vulgaris.*

(Long Island Sound specimens were identified by John C. McCain and were not examined by us. These specimens, numbering approximately 150, were collected by Clyde L. MacKenzie, Jr., from starfishes dredged at a depth of 10 m. off Pond Point, Milford, Connecticut).[2]

Commensal Relationship

C. grahami has been observed on two species of starfishes—*Asterias forbesi* (Desor) and *Asterias vulgaris* Verrill—both of which belong to the family Asteriidae. These species of *Asterias* are common in the inshore waters of southeastern Massachusetts (Sumner, Osburn and Cole, 1913; Galtsoff and Loosanoff, 1939). *C. grahami* has not yet been found on other organisms, such as algae or hydroids, with which caprellids are most commonly associated. This species clings to the starfish with the posterior pereopods in the manner characteristic of Caprellidae. The posterior three pairs of pereopods and pereods 6 and 7 lie flat against the starfish. The body bends sharply upward at the juncture of pereods 5 and 6, and the anterior section assumes various positions. The position most frequently observed is the body arched above the host; sometimes, however, specimens lie inconspicuously against the host's body between the rows of spines. When physically removed from the starfish they swim about by alternately bringing together the ends of the body and then straightening, all of which is accomplished quickly in short sequences. As many as 53 specimens of *C. grahami* were found on a single starfish (*A. forbesi*), the radius of which was 7½ cm. The density, however, varies considerably from one host to another.

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[2] Through the courtesy of J. C. McCain, this collection was subsequently examined by the authors.

This relationship appears to be very similar to that mentioned by Chevreux and Fage (1925) for *Pariambus typicus* (Krøyer). These authors reported that in European waters this caprellid occurs on *Asterias rubens* L. and *Solaster papposus* (L.).

Four specimens had a dense growth of filamentous green algae on the body and appendages anterior to pereod 5.

RELATIONSHIP OF C. GRAHAMI

Morphologically *Caprella grahami* appears to be most closely related to *C. unica* Mayer and *C. linearis* (Linnaeus). Although the latter species is larger, some of the appendages and body parts have similar shape and embellishment. Several characteristics of *C. grahami* that are useful for distinguishing it from *C. linearis* and other species are: its moderately stout body; pereods without knobs or tubercles on the dorsal surface; propodus of gnathopods 1 and 2 broad; dactyls of gnathopods and pereopods stout; absence of spines and scarcity of setae on posterior three pairs of pereopods; and the propodus of these pereopods with the palm margin not strongly concave. Also, in *C. grahami* the color is usually lighter and the pattern more uniform, whereas in *C. linearis* the color is usually darker and the pattern frequently streaked and speckled. *C. unica* is a moderately deep-water species known only from the type specimen, an immature male, collected south of Nantucket Shoals (Station 2253; 40°34′30″ N. lat., 69°50′45″ W. long.) by the U. S. Fish Commission in 1884. The stout dactyls on the gnathopods and pereopods, and the configuration of the propodus of gnathopod 2, are similar to those of *C. grahami*. *C. unica,* however, has numerous small and medium-sized spines on the dorsal and dorsolateral portions of the cephalon and pereods (Mayer, 1903).

The unique association of *C. grahami* with Asteriidae facilitates its collection and identification.

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ANNUAL PHYTOPLANKTONIC PRODUCTION IN A SYSTEM OF SHALLOW TEMPERATE ESTUARIES*

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The measurement of the primary production of phytoplankton is a matter of great interest both because of its significance to the larger problems of aquatic ecology and its importance in fishery investigations. Despite this interest the geographic distribution of such measurements in inshore areas is quite limited. Studies are largely concentrated in a few localities along the coasts of Europe and the United States, because investigators of inshore areas—such as Marshall and Orr (1927, 1930)—find it most expedient to work in the vicinity of their laboratories. These more convenient embayments are as suitable as any and the findings from them are most applicable to local fishery problems. In addition to this geographic limitation, the majority of the investigations have been restricted to a brief period during the year or have considered only photosynthesis per unit volume. Neither approach yields sufficient information to estimate annual production per unit area and thus permit comparisons of total phytoplankton production and of the efficiency with which phytoplankton production is transferred to other trophic levels. Estimates of annual phytoplankton production in inshore waters are available only for Long Island Sound (Riley, 1956) and for embayments along the coasts of Denmark (Nielsen, 1957, 1958; Grøntved, 1960) and Italy (Vatova, 1961), areas remote and different from the shallow estuaries near Beaufort, North Carolina.

Annual phytoplankton production in estuaries near the Radiobiological Laboratory in Beaufort was studied to obtain information needed for fisheries and radiobiological research and to augment current knowledge of primary production in such environments. Previous work on phytoplankton production in this area is limited to a year-long study on the Beaufort Channel (Williams and Murdoch, 1966) and a few measurements made in the same vicinity in connection with classes at Duke University Marine Laboratory (Odum and Hoskin, 1958). Aside from these, no other measurements have been made in inshore areas nearer than Baltimore Harbour (Hull, 1963) 580 km to the north and in Georgia

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* This work was carried out as part of a co-operative project of the U.S. Fish and Wildlife Service and the U.S. Atomic Energy Commission.

estuaries (Ragotzkie, 1959; Schelske and Odum, 1961) an equal distance to the south. Both of these localities are hydrographically different from that here considered.

THE AREA STUDIED

This area was a portion of the series of embayments stretching south-west from Pamlico Sound behind a chain of barrier islands, the Outer Banks (Fig. 1). The area included the eastern end of Bogue Sound, Newport River, North River, Core Sound and their interconnections, and encompassed about 400 km². Although depths in the narrow channels entering Beaufort Inlet reached 13 m, most of the area was only a metre or two deep at low tide. In many places shoals covered with less than 0·3 m of water at low tide extended out a kilometre or more from shore. Much of the shoreline consists of broad intertidal areas, some bare and others covered with salt marsh. The mean tidal range is 0·8 m close to the inlets and somewhat smaller in areas distant from them. Wind action and turbulent currents generated by the tide largely prevent the development of vertical stratification in the water. Bottom sediments are firm shell and sand close to the ocean, and become progressively softer and more muddy toward the heads of the estuaries. Benthic vegetation is most dense in shallow, sheltered locations with firm bottoms. Except after heavy rains, freshwater inflow is small in comparison with tidal exchange. Some of the fresh water, especially that entering Newport River, is

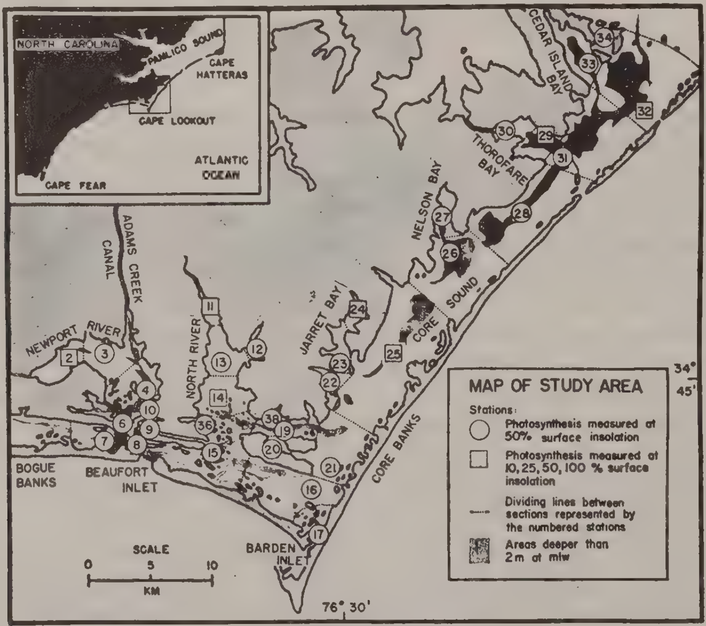
NORTH CAROLINA
PAMLICO SOUND
CAPE HATTERAS
CAPE LOOKOUT
ATLANTIC OCEAN
CAPE FEAR
CEDAR ISLAND BAY
THOROFARE BAY
NELSON BAY
ADAMS CREEK
CANAL
NEWPORT RIVER
NORTH RIVER
JARRET BAY
CORE SOUND
CORE BANKS
BOGUE BANKS
BEAUFORT INLET
BARDEN INLET
SCALE
0 5 10
KM
76° 30'
34° 45'
MAP OF STUDY AREA
Stations:
Photosynthesis measured at 50% surface insolation
Photosynthesis measured at 10, 25, 50, 100 % surface insolation
Dividing lines between sections represented by the numbered stations
Areas deeper than 2 m at mlw

Fig. 1.—Map of study area showing depth, location of sampling stations and the boundaries of the sections represented by the stations.

drained from fertilized farm land. Newport River and the eastern end of Bogue Sound also receive large amounts of domestic sewage and wastes from fish processing plants. Elsewhere in the area studied there is little pollution.

METHODS

General

Eleven surveys were made at each of 33 sampling stations between March 1964 and March 1965. The area was divided into sections on the basis of its shoreline geography and a station was located at random in each section. Data were summarized for 30 rather than 33 sections (Fig. 1 and Table I) because three sections were later combined with adjacent sections of similar hydrography. Values reported for these combined sections are averages for the two stations.

Values for mean depth and surface area of the sections (Table I) were estimated from U. S. Coast and Geodetic Survey Charts Nos 419 and 420. Mean depth was obtained by averaging the (low tide) depth at intersections in a regularly spaced grid laid over the map, and adding to this average one half the tidal range. Surface area was determined with a planimeter, using the estimated margin of the water at half tide as the shoreline. Because sections contained different surface areas, weighted averages for the study area were prepared by multiplying the values for phytoplankton production at each station by the surface of its section, and dividing the sum of the products by the total area.

The stations were sampled at approximately five-week intervals (Fig. 2). The time required for sampling varied from 7 to 11 days because the work was done from a small boat which could not operate in rough weather.

Temperature and salinity were measured *in situ* with an electrodeless induction salinometer when this instrument was available. At other times temperature was measured with a dial thermometer and salinity with a hydrometer. The Secchi disc was used to estimate light extinction. When the Secchi disc was visible on the bottom, light extinction was obtained either by extrapolation from nearby stations or from underwater photometer measurements. Extinction coefficients were obtained from Secchi disc measurements by the formula of Poole and Atkins (1929), namely, extinction coefficient $= 1\cdot 7$/Secchi disc measurement in m. Water colour was estimated from the apparent colour of the submerged Secchi disc. Insolation was measured at the laboratory with a 50-junction Eppley pyrheliometer connected to a Varian G-10 recorder.

Photosynthesis and Respiration

Photosynthesis and respiration were measured by the light and dark bottle method (Gaarder and Gran, 1927). At each station, water dipped from the surface was filtered through No. 10 bolting cloth to remove zooplankton and siphoned into three 125-ml glass-stoppered bottles. Initial oxygen concentration was determined in one bottle, and the other two were incubated for 24 h, one in the dark and one at 50% of surface insolation. Incubation was begun immediately after sampling. At 7 of the 33 stations, additional bottles of water were incubated for 24 h at 10, 25, and 100% of surface insolation (Fig. 1). Dissolved oxygen was measured by Winkler titration, following generally the procedures of Strickland and Parsons (1960), and changes in oxygen concentration were used to estimate the production of organic carbon by the relationship formulated by Ryther (1956), namely, 1·0 mg oxygen is equivalent to 0·30 mg carbon.

Selection of the period of incubation and the levels of insolation was based on previous studies in the area (Williams and Murdoch, 1966). Incubation for 24 h usually produced changes in dissolved oxygen large enough to be detected by the methods used, but not so large as to markedly alter conditions within the bottles. The rate of respiration was constant for at least 24 h. Fifty per cent of surface insolation usually approximated the amount yielding maximum photosynthesis over an entire day, and was selected therefore as the standard illumination to which light bottles from all the stations were exposed.

Light bottles were incubated in open trays positioned to receive maximum insolation. The trays were constructed with lucite sides and non-reflective black bottoms. Light was attenuated to 10, 25 and 50% of surface insolation by passage through one or more layers of plastic screen. Temperature was controlled by immersing both light and dark bottles in running sea water. Silt which settled on to the light bottles was rinsed off periodically.

These methods of incubation exposed the samples collected in any individual survey to widely different regimes of temperature and insolation. Variations in cloud cover during the several days required for the survey often produced large differences in the total energy available for phytoplankton photosynthesis in samples incubated at different times. In individual surveys, the minimum total energy reaching bottles at the same percentage of surface insolation during the 24 h of incubation ranged from 25 to 90% of the maximum, and averaged 78%. Samples taken at different times were in addition often exposed to different maximum, minimum, and average temperatures because the boat carrying the incubators traversed waters of widely different temperature in the course of a survey (Fig. 2). These procedures were thought preferable to incubation under artificially uniform conditions because the purpose of this study was estimation of total phytoplankton production in the area rather than the geographic distribution of potential phytoplankton production.

RESULTS

Temperature, Salinity, and Transparency

Average temperature followed a normal seasonal cycle, ranging from 27·6°C in June to 7·9°C in January (Fig. 2). However, large variations in temperature were present during most of the surveys (Fig. 2) because the shallowness of some areas permitted the water to change temperature rapidly in response to variations in weather. Shallow embayments of similar hydrography occasionally differed by as much as 5°C when sampled a few days apart. During the spring and fall, the heads of estuaries sometimes differed from their mouths by 7 to 8 °C because deep channels close to the inlets change temperature more slowly than the shallow areas further up the estuaries. Temperature at the head of North River (Station 11) ranged from 4 to 30 °C, whereas temperature in Bardens Inlet (Station 17) close to the ocean ranged from 10 to 28 °C. Despite variations present during individual surveys, average temperatures for the stations were similar. In warm weather (May 5 to Sept. 21) averages ranged from 25 to 27 °C, and in cool weather (Sept. 22 to May 4), from 12 to 15 °C.

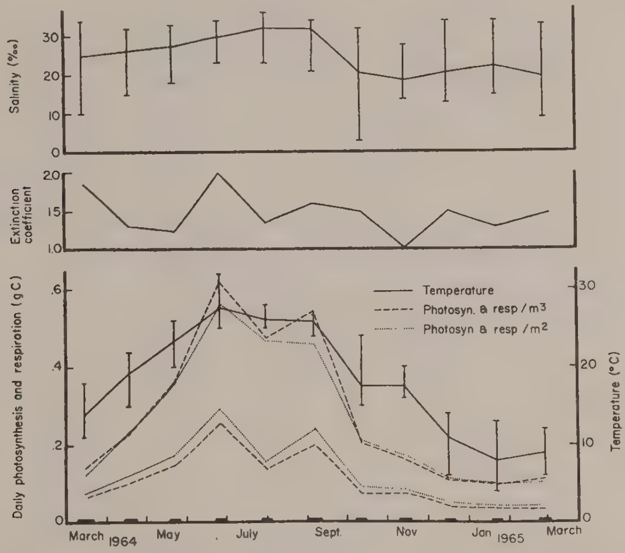

Fig. 2.—Average values for each survey for salinity, extinction coefficient (per metre), water temperature, and daily rates of gross photosynthesis (upper curves) and respiration (lower curves). Vertical bars on the temperature and salinity curves indicate the range of values present; thickened segments of the abscissa indicate the duration of the surveys.

The distribution of salinity was variable (Fig. 2 and Table I). Close to the ocean, salinities were high, usually at least 30‰. During a dry period, midsummer of 1964, salinities at the heads of the estuaries rose to between 20 and 30‰ from the combined effects of evaporation and intrusion of oceanic water. After heavy rains, such as those accompanying the hurricanes during the fall of 1964, the high salinity water was pushed out. Between the September and October surveys, average salinity in the area dropped from 31·8 to 20·5‰ and salinity at the head of the Newport River (Station 2) from 21 to 3‰. Even at the western end of Core Sound (Station 32), a location remote from sources of both fresh and oceanic water, salinity ranged from 13 to 29‰. Areas receiving freshwater drainage, Stations 2, 11, 12, 24 and 30, were usually orange to brown because inflowing fresh water was stained with seepage from swamps. Areas of high salinity close to the inlets, Stations 6, 7, 8, 16 and 17, were usually green. Predominately yellowish green water was present elsewhere.

The estuarine water was turbid in comparison with the ocean, but like temperature and salinity, the amount of turbidity in the estuaries was quite variable (Fig. 3 and Table I). Extinction coefficients were lowest close to the ocean, and increased steadily toward the heads of the embayments receiving freshwater drainage (Table I). Part of this increase was due to the brown material in the water and part to the character of the bottom sediments, which changed from sand and shell close to the ocean, to muddy sand, and finally to flocculent ooze

TABLE I

Hydrographic and physical data; areas and depths of the sections represented by the stations are for half tide; average values for salinity and extinction coefficient are for the periods May 5 *to Sept.* 21, *and Sept.* 22 *to May* 4

Station number	Area and depth of section		Salinity (‰)		Extinction coefficient	
	Area (km²)	Mean depth (m)	May–Sept.	Sept.–May	May–Sept.	Sept.–May
2	9·8	0·7	24	13	8·5	5·9
3	12·0	1·0	31	19	2·6	2·2
4	14·8	0·9	31	24	1·4	1·2
6 + 8	3·9	4·1	33	29	1·0	1·1
7	5·7	1·5	32	31	1·0	1·2
9 + 10	1·0	1·5	32	24	1·1	1·3
11	3·1	0·6	26	19	3·2	2·6
12	1·7	0·7	28	20	2·4	2·1
13	10·3	0·7	30	22	1·8	1·7
14	11·4	0·9	31	23	1·4	1·2
15	28·4	1·6	32	27	1·2	1·2
16	25·5	1·0	33	25	1·2	0·9
17	6·1	1·1	34	31	0·7	0·8
19 + 38	8·0	1·0	33	23	1·4	1·1
20	1·7	0·7	32	23	1·8	1·0
21	22·4	0·9	34	25	1·1	1·0
22	3·6	0·9	31	20	2·1	1·4
23	4·5	0·9	31	22	1·8	1·1
24	3·4	0·4	28	17	2·8	1·5
25	58·7	1·0	33	22	1·2	1·0
26	37·0	1·2	30	20	1·2	1·2
27	5·1	1·1	30	19	1·8	1·1
28	23·7	1·2	28	19	1·2	1·6
29	6·8	2·1	27	18	1·2	1·3
30	3·2	1·5	24	16	1·9	1·5
31	30·3	1·5	27	19	1·3	1·4
32	36·0	1·4	26	18	1·2	1·6
33	11·2	1·2	23	16	1·2	1·2
34	4·2	0·7	22	15	1·4	1·8
36	1·1	0·8	32	23	1·5	1·4
Average	—	—	30	21	—	—
Weighted average	—	1·18	—	—	1·52	1·42

as areas of fresh water are approached. These softer sediments are easily suspended by wave action and tidal currents. Thus each extinction coefficient was a product of both location and environmental conditions at the time of measurement. Average extinction coefficients for the area ranged from 1·0 to 2·0 and had no obvious seasonal cycle (Fig. 2).

Photosynthesis at 50% Insolation and Respiration per Unit Volume

There was a pronounced seasonal cycle in photosynthesis and respiration which closely paralleled the cycle in water temperature. In weighted averages for the

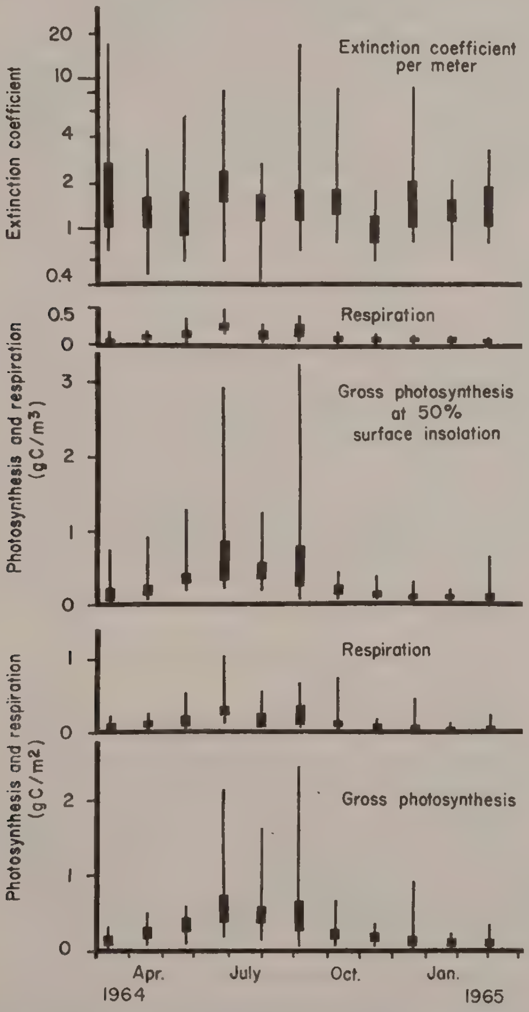

Fig. 3.—Range and distribution of measurements of extinction coefficient, respiration, and gross photosynthesis in each of the surveys. The thickened segments indicate a range centred around the weighted average and containing about one half the observations.

individual surveys (Fig. 2) daily photosynthesis at 50% of surface insolation ranged from 97 to 622 mg C/m^3 and daily respiration from 35 to 256 mg C/m^3. Lowest rates occurred in January through March when water temperatures were low, and highest rates in June when temperatures were high. Rates averaged around three times greater in warm weather (May to September) than in cool weather (September to May) (Table II). There were no irregularities in the cycle except for a dip in midsummer. These weighted averages form good estimates of conditions over the area because, despite the wide range of the values obtained in each survey, the majority lay close to these averages (Fig. 3). At almost every station the mean rates for respiration and photosynthesis were two- to five-fold greater in warm weather than in cool weather (Table II).

The broad range of rates observed in each survey undoubtedly arose partly from non-uniform conditions during incubation, but the variation was so systematically distributed with respect to hydrography that it clearly reflected consistent differences among the stations. Photosynthesis throughout the year and respiration in warm weather were most intense at the heads of Newport and North Rivers, both shallow, turbid areas receiving freshwater inflow. In the lower portions of these estuaries and in other areas distant from large freshwater influx, rates were generally much lower (Table II). At the head of Newport River (Station 2), the least saline portion of the area, daily photosynthesis and respiration in early September reached 3·29 and 0·52 g C/m^3, respectively. In warm weather, photosynthesis at Station 2 averaged nine times greater than at the least productive stations, and in cool weather, four times greater (Table II). Respiration was less variable than photosynthesis; the highest average value for warm weather (Station 2) was only three times the lowest. Average respiration in cool weather had only a twofold variation and was not obviously correlated with hydrography. Despite the occurrence of high rates of photosynthesis and respiration, however, in areas of low salinity and high turbidity, average rates of photosynthesis and respiration of the individual surveys were uncorrelated with the average extinction coefficient and had highly significant positive correlations with average salinity (Fig. 2).

Vertical Distribution of Photosynthesis

Measurements of photosynthesis at the four levels of insolation, 10, 25, 50 and 100%, made at seven stations (Fig. 1) were used to estimate the vertical distribution of photosynthesis at all the stations. Values for relative photosynthesis at these four levels of insolation were pooled into a single curve (Fig. 4) because there were no seasonal or regional patterns. Measurements at each have been expressed as percentages of photosynthesis at 50% insolation. The logarithms of the percentages were averaged for each level of insolation and the antilogs of the means then plotted at the depth each would occupy with an extinction coefficient of unity, and joined with a smooth curve (Fig. 4). The curve was extended below the level of 10% insolation by assuming that photosynthesis was directly proportional to illumination at these lower intensities. Photosynthesis averaged slightly greater at 50% insolation than at 25 or 100%.

TABLE II

Gross photosynthesis and respiration; average daily values are for the periods May 5 to Sept. 21, and Sept. 22 to May 4; average annual values are for 140 warm period and 225 cool period days

Station number	Daily Photosynthesis at 50% insolation and respiration (g C/m³)				Daily Photosynthesis and respiration (g C/m²)				Annual Photosynthesis and respiration (g C/m²)	
	May–Sept.		Sept.–May		May–Sept.		Sept.–May			
	Photosyn.	Resp.	Photosyn.	Resp.	Photosyn.	Resp.	Photosyn.	Resp.	Photosyn.	Resp.
2	2·20	·40	·43	·08	·68	·28	·23	·06	147	53
3	·85	·23	·29	·08	·64	·23	·22	·08	139	50
4	·78	·22	·25	·08	·65	·20	·21	·07	138	44
6+ 8	·70	·18	·17	·08	1·62	·74	·42	·33	321	178
7	·47	·19	·15	·05	·65	·28	·20	·08	136	57
9+10	·93	·26	·22	·06	1·20	·39	·28	·09	231	75
11	1·00	·32	·32	·07	·52	·19	·17	·04	111	36
12	·56	·28	·18	·07	·41	·20	·12	·05	84	39
13	·63	·24	·19	·05	·46	·17	·12	·04	91	33
14	·44	·19	·21	·05	·37	·17	·18	·04	92	33
15	·55	·19	·18	·05	·75	·30	·25	·08	161	60
16	·37	·14	·10	·05	·35	·14	·08	·05	67	31
17	·33	·18	·13	·05	·39	·20	·13	·06	84	42
19+38	·47	·15	·14	·06	·44	·15	·14	·06	103	35
20	·40	·14	·11	·05	·24	·10	·07	·04	49	23
21	·26	·19	·10	·07	·22	·17	·08	·06	49	37
22	·38	·15	·11	·06	·30	·13	·10	·05	64	29
23	·41	·18	·12	·07	·34	·16	·11	·06	72	36
24	·41	·20	·10	·05	·15	·08	·04	·02	30	16
25	·45	·14	·11	·04	·42	·14	·11	·04	84	29
26	·30	·18	·11	·08	·34	·22	·12	·10	75	53
27	·37	·16	·12	·07	·36	·18	·12	·08	77	43
28	·44	·12	·18	·07	·48	·14	·19	·08	110	38
29	·34	·21	·11	·06	·58	·44	·18	·13	122	91
30	·40	·22	·10	·05	·44	·33	·13	·08	91	64
31	·38	·20	·11	·07	·48	·30	·14	·11	99	67
32	·35	·22	·17	·08	·43	·31	·20	·11	105	68
33	·39	·24	·17	·10	·43	·29	·19	·12	103	68
34	·24	·16	·21	·08	·16	·11	·13	·06	52	29
36	·80	·20	·17	·04	·60	·16	·13	·03	113	29
Weighted average	·501	·186	·139	·064	·464	·214	·154	·076	99·6	47·1

Values from this graph were used to convert measurements of photosynthesis at 50% insolation into estimates of photosynthesis per square metre. The percentage of insolation reaching the mean depth for the section (Table I) was calculated from the extinction coefficient. For stations where more than 0·5% penetrated to the bottom, photosynthesis at 50% insolation was multiplied by the mean depth of the section and by a factor which expressed average photosynthesis per m^3 for the entire water column as a percentage of photosynthesis occurring at 50% insolation. The value for this factor was selected from the dotted

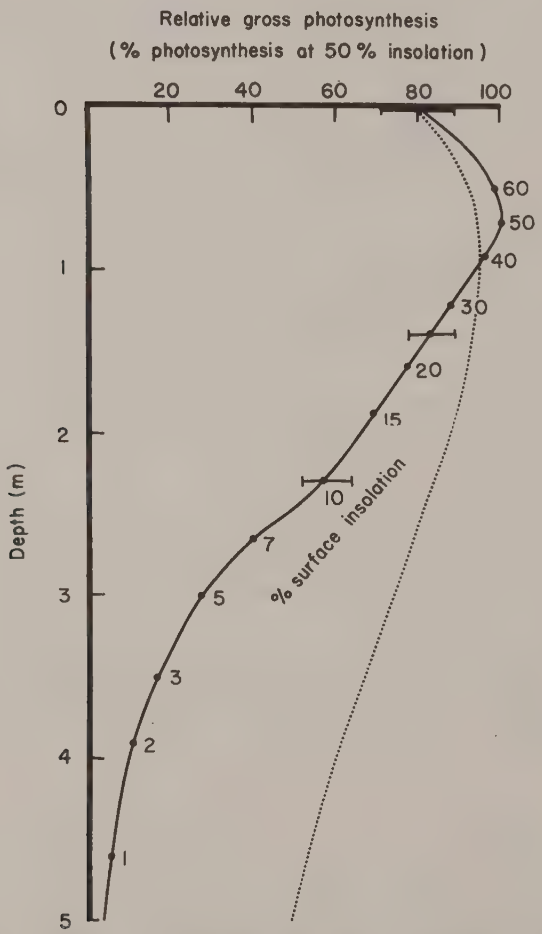

Fig. 4.—Vertical distribution of insolation and relative gross photosynthesis with an extinction coefficient of unity; continuous line, average photosynthesis as a percentage of that at 50% insolation; cross bars indicate 95% confidence limits around the means; dotted line, average photosynthesis of a water column extending upward from that depth as a percentage of photosynthesis at 50% insolation.

line in Figure 4 according to the percentage of light reaching the bottom. The dotted line was obtained by determining the integral of the curve for relative photosynthesis (the solid line) for a series of depths, dividing each integral by the depth it represented, and joining the quotients with a smooth curve.

At stations where less than 0·5% insolation reached the bottom, photosynthesis per square metre was calculated by multiplying photosynthesis at 50% insolation by a factor obtained by dividing the extinction coefficient into 2·52 m. This value, 2·52 m, was the integral of the curve for relative photosynthesis down to zero light and represented photosynthesis per m^2 for the entire water column divided by photosynthesis per m^3 at 50% insolation, when the extinction coefficient was unity. Division of 2·52 m by the extinction coefficient scaled the factor to fit the existing water transparency.

The use of mean depth in the calculations for each section yielded satisfactory estimates of photosynthesis per m^2 because the ratio of average photosynthesis per m^3 for the water column to photosynthesis at 50% insolation did not change rapidly with depth (Fig. 4). Between the surface and the depth of 5% insolation, the value of this ratio ranged from 75% to 95%; even at 1% insolation the ratio was still 53%.

Photosynthesis and Respiration per Unit Area

Seasonal cycles for photosynthesis and respiration per m^2 were similar to those for photosynthesis and respiration per m^3. Weighted averages of the rates per m^2 for the individual surveys were numerically similar to those for rates per m^3 because the average depth of the area studied was close to 1 m (Fig. 2). The rates per m^2 in most sections averaged two to five times greater in warm weather than in cool, and the weighted averages of these rates for the entire area studied, three times greater in warm weather than in cool (Table II). The weighted averages for rates per m^2, like those for rates per m^3, represent conditions in the area because the majority of the values were close to the average for the survey (Fig. 3).

The areal distribution of rates per m^2 was very different from that for rates per m^3 (Table II). Highest rates of photosynthesis and respiration per m^2 were in the sections near the Beaufort Inlet containing the deep channels (Figs 5 and 6). There, although rates per m^3 were only moderately high, the mean depth was 4·1 m and the transparency extended the euphotic zone, i.e. the depth of 1% insolation, at times to 11 m. The heads of North and Newport Rivers and other areas of most intense photosynthesis and respiration were so shallow that rates per m^2 were lower than in the deep channels. The highest daily rate of photosynthesis per m^3, 3·29 g C at Station 2 in September, produced only 0·49 g C/m^2 because the euphotic zone was only 0·27 m deep. Photosynthesis per m^2 was scarcely more variable than that per m^3 at 50% insolation (Fig. 3 and Table II) because in general the shallower sections had higher rates per unit volume than the deeper sections which compensated for the shorter water columns. The lowest rates per m^2 were mostly in shallow areas lacking large influx of fresh water. Respiration per m^2, unlike photosynthesis, was three to four-fold more variable than that per m^3 (Fig. 3 and Table II) because there was no significant negative

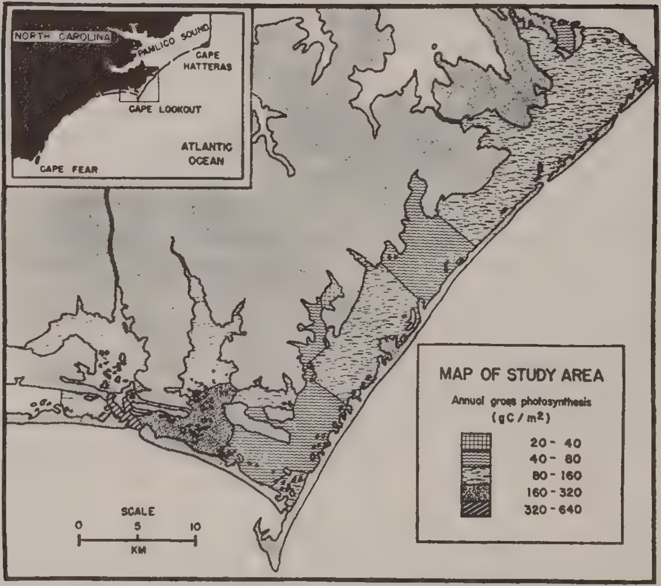
NORTH CAROLINA
PAMLICO SOUND
CAPE HATTERAS
CAPE LOOKOUT
ATLANTIC OCEAN
CAPE FEAR
MAP OF STUDY AREA
Annual gross photosynthesis
(gC/m²)
20 - 40
40 - 80
80 - 160
160 - 320
320 - 640
SCALE
0 5 10
KM

Fig. 5.—Areal distribution of annual gross photosynthesis.

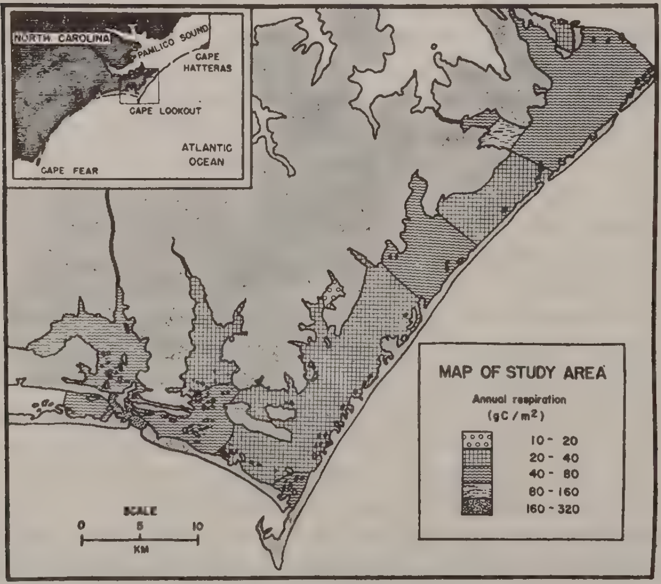
NORTH CAROLINA
PAMLICO SOUND
CAPE HATTERAS
CAPE LOOKOUT
ATLANTIC OCEAN
CAPE FEAR
MAP OF STUDY AREA
Annual respiration
(gC/m²)
10 - 20
20 - 40
40 - 80
80 - 160
160 - 320
SCALE
0 5 10
KM

Fig. 6.—Areal distribution of annual respiration.

correlation between rate per m^3 and mean depth of the section. The highest rates per m^2 were in the deeper sections and the lowest in the shallower sections.

The average daily rates for the sections summed for a year containing 140 warm period and 225 cool period days yielded annual rates of photosynthesis ranging from 30 to 321 g C/m^2 and of respiration ranging from 16 to 178 g C/m^2 (Table II). In most of the sections, photosynthesis lay between 80 and 160 g C/m^2 (Fig. 5) and respiration between 20 and 80 g C/m^2 (Fig. 6). Weighted averages for gross photosynthesis and respiration were 99·6 and 47·1 g C/m^2, respectively. Thus on an annual basis, net photosynthesis was approximately half the gross photosynthesis.

DISCUSSION

Phytoplankton production in these shallow embayments presents a paradoxical picture. Under favourable light conditions daily production per unit volume appears high or even very high in comparison with much of the open sea (Strickland, 1960; Ryther, 1963), but the intensity of photosynthesis does not fully compensate for the shallowness of the water, and production per unit area is relatively low. Precise comparisons of my results with those obtained elsewhere are difficult for two reasons. Many of the values in the literature for phytoplankton production were obtained by the ^{14}C method which appears to measure the increase in particulate organic carbon rather than in total organic carbon, the quantity estimated by the oxygen method (Antia et al., 1963), and yield values between net and gross photosynthesis (Strickland, 1960). In addition many studies do not cover enough of the year to permit estimation of annual values. Data from various studies are summarized in Table III, with values re-calculated where necessary to obtain grams of carbon per m^2. These data suggest that average annual production in the present area was similar to that of bays in Denmark and of a mid-ocean area, the Sargasso Sea, but below that of the Atlantic Ocean off Long Island. Values for both gross and net photosynthesis in a deep inshore area, Long Island Sound, were more than three times the *averages* for this area, but similar to those for the deepest and most productive sections. Daily rates of gross photosynthesis in the area were generally below those reported elsewhere.

The substantial amount of net production in the area contrasts with estimates of daily rates from other shallow embayments (Table III). Low net production stems either from low gross production, as in the vegetated bays in Texas, or from high respiration, as in the other Texas bays and the Georgia and the Long Island estuaries. Respiration per unit area in excess of photosynthesis arises either from a high rate of respiration per unit volume or from a water column much deeper than the euphotic zone, or from a combination of both. The data of Barlow, Lorenzen and Myren (1963) and of Ragotzkie (1959) suggest that negative net photosynthesis in the Long Island and the Georgia estuaries was derived from the combination of rapid respiration of allochthonous material with a shallow euphotic zone. (The data of Odum and Hoskin (1958) on the Texas bays are insufficient for speculating on the origin of the negative net photosynthesis.)

TABLE III

Comparison of daily and annual rates of phytoplankton photosynthesis in the area studied with those from other marine environments

Environment	Depth (m)	Season	Method of measurement	Rate of photosynthesis (g C/m²)			Reference
				Gross photosyn.	Net photosyn.	Between net and gross photosyn.	
				Annual Values			
Estuaries, N. C.	1·2	—	O_2	99·6	52·5		This work
Bays, Denmark	1–33	—	^{14}C			6–105, ave. 58	Nielsen, 1957, 1958
		—	O_2	39–175			Nielsen, 1957, 1958
Sargasso Sea	2700	—	^{14}C			72	Menzel and Ryther, 1960
Atlantic Ocean off Long Island							
Continental Shelf	<50	—	^{14}C			165	Ryther, 1963
Continental Slope	>1800	—	^{14}C			120	Ryther, 1963
Long Island Sound	25	—	O_2	380	170		Riley, 1956
				Average Daily Values			
Estuaries, N.C.	1·2	May–Sept.	O_2	0·46	0·25		This work
		Sept.–May	O_2	0·15	0·08		This work
Bays with benthic plants, Texas	ca. 1	Various	O_2	0·10	0·03		Odum and Hoskin, 1958
Bays, Texas	ca. 1	Mostly summer	O_2	0·55	–0·01		Odum and Hoskin, 1958
Harbor, Baltimore, Md.	5–12	Aug.–Oct.	O_2	0·9			Hull, 1963
Polluted estuary, Long Island	1–2	Mar.–Sept.	O_2	2·4	–0·5		Barlow, et al., 1963
Estuary, Georgia	3–5	Various	O_2	0·7	–0·1		Ragotzkie, 1959
Corpus Christi Bay, Texas	3	June–July	O_2 diurnal curve	3·3			Odum and Wilson, 1962

The present area, unlike the estuaries in Georgia and Long Island, is in general sufficiently shallow and transparent to permit net photosynthesis down to the bottom. The mean depth of the water, 1·18 m, is less than the 1·7 m which would produce maximum net photosynthesis with the annual average transparency and rates of photosynthesis and respiration. This optimal depth, calculated from data in Figure 4 and Table II, is the level where gross photosynthesis equals respiration. Increase of the mean depth from its actual value to this optimal value would increase net photosynthesis only about 15%, if all other factors remained constant. If mean depth were increased to 4·0 m, annual gross photosynthesis would approach 160 g C/m^2, the maximum value possible. Net photosynthesis for this 4·0 m water column would be zero.

Transparency in this area is also less than that yielding maximum net photosynthesis. With the average vertical distribution of photosynthesis (Fig. 4) the extinction coefficient yielding maximum gross and thus net photosynthesis for a 1·18 m depth is 0·76. Reduction of the extinction coefficient from its actual value, about 1·5, to this optimal value would elevate net photosynthesis 8% if all other conditions remained unchanged. Thus neither of these two hypothetical modifications of the area, increased transparency and increased depth, could separately increase net photosynthesis very much, suggesting that these aspects of the environment are on the average nearly optimal for achieving a maximum ratio of net to gross photosynthesis.

The pronounced seasonal cycle present during both this study and a preceding one in the Beaufort Channel (Williams and Murdoch, 1966) may arise from a seasonal change in the availability of nutrients. Such cycles in photosynthesis, with markedly higher levels in warm weather, have also been observed in Long Island Sound and in shallow bays along the coasts of Denmark, Italy, and Massachusetts, and their occurrence ascribed to more rapid regeneration of nutrients from the bottom due to increased bacterial metabolism at higher temperatures (Riley, 1941, 1956; Nielsen, 1958; Grøntved, 1960; Vatova, 1961; Ryther, 1963).

Differences in the influx of nutrients may account for areal differences in the intensity of photosynthesis because the sections with highest rates of photosynthesis per m^3 (Table II) received either drainage from fertilized farm land, or large amounts of raw sewage, or both. Influx of fresh water from regions with little agriculture into Jarret, Nelson, and Thorofare Bays did not produce intense photosynthesis. A number of other factors, temperature, salinity, growth of benthic plants and rate of tidal flushing, which might modify the intensity of photosynthesis are not correlated with its areal distribution here. The areal distribution of one additional factor, rate of grazing, is unknown. However, grazing by zooplankton is unimportant (Williams, 1965), and it seems unlikely that differences in the abundance of fish (menhaden) and benthic filter-feeders would sufficiently alter the abundance of phytoplankton to produce the observed variation in photosynthesis.

The absence of any evidence for brief plankton blooms in either this study or a preceding one in the Beaufort Channel may be due to the special characteristics of the area rather than to the widely spaced surveys. Blooms of phytoplankton, other than those caused by aggregations of motile cells, arise from the sudden introduction of nutrient rich water into the euphotic zone, and are terminated either by a disappearance of nutrients or by the grazing of zooplankton populations which have increased in the presence of greater food supplies. The shallow character and lack of stratification in the area preclude conditions for initiation of a bloom, and the scarcity of zooplankton relative to phytoplankton production suggests that their grazing does not control the abundance of phytoplankton.

The plankton production measured in the Beaufort Channel (Stations 9 and 10) during this study was much like that of the preceding year except for the 60% higher average rates in warm weather for photosynthesis and respiration, (Williams and Murdoch, 1966). The average rates of photosynthesis and of respiration in cool weather, and the periods of high and low production, were similar during the two years. Even average relative rates of photosynthesis at percentages of surface insolation for the area (Fig. 4) were close to those in the Beaufort Channel during the previous year. Similarities between observations at this single locality during two successive years suggest that values obtained in the present study may be characteristic of the area.

ACKNOWLEDGMENTS

The successful completion of this study required the advice and assistance of many individuals at the Radiobiological Laboratory. I am particularly grateful for the unfailing co-operation I received from those regularly assisting with the field and laboratory work: Mrs M. B. Murdoch, W. D. C. Smith, L. K. Thomas, and T. G. Roberts.

SUMMARY

Temperature, salinity, transparency, and phytoplankton photosynthesis and respiration have been measured for a year in a system of estuaries near Beaufort, N.C. These estuaries had an area of ca. 400 km^2, a maximum depth of 13 m and a mean depth of 1·18 m. The water was usually unstratified. Average temperature ranged from 27·6 °C in June to 7·9 °C in January. Near the ocean, salinities were usually over 30‰; at the heads of the estuaries, salinities were at least 20‰ in dry weather, but dropped to low values after heavy rain. Extinction coefficients varied widely over the estuaries; the averages ranged from 1·0 to 2·0.

Photosynthesis and respiration, measured by changes in dissolved oxygen in light and dark bottles, had a marked seasonal cycle paralleling the cycle in water temperature. Average daily gross photosynthesis at 50% of surface insolation ranged from 97 to 622 mg C/m^3 and average daily respiration from 35 to 256 mg C/m^3. Rates of photosynthesis and respiration per m^3 were usually greatest in the shallow, turbid water at the heads of the estuaries.

The vertical distribution of photosynthesis, obtained from measurements made at 10, 25, 50 and 100% of surface insolation, indicated that daily photosynthesis

was maximal at about 50% of surface insolation. Photosynthesis per square metre was calculated from estimates of mean depth of the estuaries and ratios of average rates of photosynthesis for entire water columns to the rate of photosynthesis at 50% insolation. Average values for photosynthesis and respiration per m^2 followed seasonal cycles similar to those of photosynthesis and respiration per m^3. However, rates per m^2 were usually greatest in the deep channels near the mouths of the estuaries. Daily photosynthesis averaged 464 mg C/m^2 in warm weather (May through September) and 214 mg C/m^2 in cool weather (September through May); daily respiration averaged 154 mg C/m^2 in warm weather and 76 mg C/m^2 in cool weather. These daily rates summed for a year of 140 warm and 225 cool days yielded annual rates of 99·6 g C/m^2 for gross photosynthesis and 47·1 g C/m^2 for respiration.

The rates of phytoplanktonic photosynthesis in the estuaries are considered in relation to possible controlling factors and are compared with values reported from other marine environments. Gross photosynthesis per m^2 was less than that of the Atlantic Ocean off Long Island and of many inshore areas. Net photosynthesis per m^2, however, was greater than most of the values from other environments because conditions approached those producing a maximum ratio of net to gross photosynthesis.

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Physiology of *Mnemiopsis* in Relation to Its Role as a Predator

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Physiological research was done on the common estuarine ctenophore, *Mnemiopsis leidyi,* to evaluate its importance as a predator on zooplankton. Respiratory rates, measured by changes in dissolved oxygen, were directly proportional to the volumes of the live animals over a size range of 1 to 23 ml. At 10 C, daily respiration ranged from 0.06 to 0.11 mg 0_2/ml volume, and averaged 0.08. The Q_{10} for respiration was 2.3. Comparison of these measurements with data on the chemical composition and abundance of zooplankton suggested that at times grazing by *Mnemiopsis* may be important. In the estuaries near Beaufort, N. C., the organic carbon required each day by a *Mnemiopsis* 20 ml in volume is equivalent to the zooplankton contained in 4 to 100 liters of water.

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R. B. WILLIAMS and M. B. MURDOCH, Radiobiological Laboratory, Beaufort, North Carolina. **Annual Production of *Spartina* and *Juncus* in North Carolina Salt Marshes.**

The production of organic matter by aerial portions of two phanerogams, *Spartina alterniflora* and *Juncus roemerianus,* was measured in marshes near Beaufort, N. C. Living and dead plants were removed from 1 m^2 quadrats at 5-week intervals, sorted, dried and weighed. In September, the end of the main growing season, standing crops of mature *Spartina* ranged from 0.25 kg/m^2 (dry weight) in the high marsh to 2.1 kg/m^2 in streamside marsh, and were closely correlated with the average height of the plants. Production of *Spartina* calculated by adding an estimate of the quantity of leaves produced and lost prior to harvest to the measured standing crop of living plants was found to average ca. 120% of the standing crop. The maximum standing crop and annual production of *Juncus* were ca. 1 kg/m^2. From these rates of production and the quantities of dead plant material in the quadrats, the daily loss from the marsh of dead *Spartina* was estimated to average 1% of its total weight, and of dead *Juncus,* 0.1%.

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PHYTOPLANKTON PRODUCTION AND CHLOROPHYLL CONCENTRATION IN THE BEAUFORT CHANNEL, NORTH CAROLINA[1]

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ABSTRACT

A yearlong study was conducted on phytoplankton at the mouth of a shallow estuary. Photosynthesis had a pronounced seasonal cycle, without major irregularities, that followed the cycle in water temperature. Gross photosynthesis at the surface ranged from 0.12 to 0.72 mg C liter^{-1} day^{-1}. Daily photosynthesis at 50, 25, and 10% of surface illumination averaged 104, 85, and 58% of the surface value. Respiration ranged from 0.01 to 0.29 mg C liter^{-1} day^{-1} and averaged 40% of surface gross photosynthesis. Annual gross production was 113 g C/m^2 for a 1.0 m water column (average depth of the estuary) and 225 g C/m^2 for the entire euphotic zone. Annual respiration was 0.39 g C/m^3. This low production was ascribed to shallowness and turbidity.

The phytoplankton was chiefly nannoplankton (centric diatoms) and averaged 2×10^6 cells/liter. Nannoplankton also contained most of the chlorophyll *a* and produced most of the respiration and photosynthesis.

Chlorophyll *a* ranged from 2.0 to 9.3 μg/liter, and averaged 3.6 μg/liter from June to October (the period of high water temperatures and high production) and 4.8 μg/liter the remainder of the year. The ratio of photosynthesis to chlorophyll *a* (at the surface during daylight hours) ranged from 1.9 to 19.8 mg C(mg Chl a)$^{-1}$ hr^{-1} and followed water temperature. Values were predicted by the equation:

$$\log\,[\text{mg C }(\text{mg Chl } a)^{-1}\,\text{hr}^{-1}] = 0.138 + 0.0353 \times \text{temperature }(^\circ\text{C}),$$

yielding a Q_{10} of 2.25 for the ratio of photosynthesis to chlorophyll *a*.

INTRODUCTION

Much of the southeastern seaboard of the United States is shallow estuaries. This habitat appears to be biologically productive since it supports substantial fisheries. There are, however, few quantitative data concerning the primary production which ultimately sustains these fisheries. The purposes of our yearlong study in the Beaufort Channel were to characterize approximately an estuarine phytoplankton population, to measure its production, and to determine the usefulness of chlorophyll *a* concentration as a means to estimate productivity of this population.

Previous work on the phytoplankton of the Beaufort area was limited to taxonomic studies of the diatom flora by Hustedt (1955), Manly (1953), and Wolfe (1930), and to a few measurements of photosynthesis made in connection with classes at Duke University Marine Laboratory (Bartell 1959; Odum and Hoskin 1958). There are no quantitative studies of estuarine phytoplankton for areas nearer to Beaufort than Chesapeake Bay 300 km to the north (Hull 1963; Patten, Mulford, and Warinner 1963; Patten et al. 1964) and the coast of Georgia 600 km to the south (Ragotzkie 1959; Schelske and Odum 1961). None of these studies treat both the standing crop of phytoplankton and their annual rate of production.

Since chlorophyll *a* is essential for photosynthesis and is easily measured, numerous attempts have been made to relate its concentration to the rate of photosynthesis of phytoplankton populations (Ryther and Yentsch 1957, 1958; Strickland 1960). Although values for gross photosynthesis at optimal illumination tend to cluster around 4 g C (g Chl a)$^{-1}$ hr^{-1}, the range for these values is so broad that measurements of pigment provide only a very crude estimate of primary production. However, since values in the literature were obtained from widely scattered locations representing a variety of habitats, it seemed possible that the ratio of photosynthesis to chlorophyll *a* would be less variable among samples from a single location.

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[1] The work reported was carried on as a part of a cooperative project of the U.S. Fish and Wildlife Service and the U.S. Atomic Energy Commission. Publication has been approved by these agencies.

Description of area

The Beaufort Channel is the smaller of two passageways connecting the broad, shallow estuary of the Newport River with the Beaufort Inlet and thus with the ocean. The channel is 90 to 400 m wide, 3 km long, and 4 to 10 m deep. The tide, with a mean amplitude of 0.8 m, generates turbulent currents in the channel swift enough to carry sand grains to the surface from depths of several meters. The estuary of the Newport River is over 6 m deep in a few channels, but averages only 0.8 m at low tide and 1.3 m at high tide. Its surface area at low tide is 3.6 km^2 and at high tide 5.0 km^2. Its volume at low tide is approximately half that at high tide. The ocean near the Beaufort Inlet is also relatively shallow; the 20-m isobath lies 15 km offshore. Bottom sediments in both the Beaufort Channel and the estuary range from mud to sand. Much of the intertidal area is salt marsh; there is little development of submerged macroscopic plants. Except after heavy rains, freshwater inflow in the area is minor in comparison with the tidal exchange. The Newport River drains a mixture of forest and agricultural lands; the estuary and the Beaufort Channel receive wastes from fish processing plants and raw sewage from communities totaling several thousand people.

MATERIALS AND METHODS

Our study consisted of 26 measurements made from December 1962 to December 1963. Water samples were dipped from the surface of the Beaufort Channel at Pivers Island at approximately the same time of day (0900) at one- and three-week intervals; thus spaced, successive measurements were at approximately opposite stages of the tide. A surface sample was representative of the entire water column because turbulence produced by tidal currents largely precluded stratification. The samples were strained through No. 10 netting to remove zooplankton and part of the water was refiltered through No. 25 netting to remove the net plankton. The No. 25 netting had openings ca. 60 μ square that retained the largest cells and chains of small cells. Photosynthesis, respiration, and the standing crop of plankton were estimated separately for the coarsely filtered and the finely filtered water to determine the relative importance of the net and nannoplankton. When the samples were taken for productivity measurements, water temperature was measured to the nearest degree with a dial thermometer and salinity to the nearest part per thousand with a hydrometer. Secchi disc readings were made daily.

Photosynthesis and respiration were measured by the light- and dark-bottle technique of Gaarder and Gran (1927). Dissolved oxygen was measured by Winkler titration, following generally the procedures of Strickland and Parsons (1960). Changes in dissolved oxygen were converted to changes in organic carbon using the relationship formulated by Ryther (1956): 1.0 mg oxygen is equivalent to 0.30 mg carbon.

Seawater was siphoned into 125-ml glass-stoppered bottles. Three dark bottles were placed in running seawater for 24 hr, and two light bottles were suspended at each of four depths in the Beaufort Channel for the same period. This period of incubation produced, in general, changes in the concentration of dissolved oxygen large enough to be readily measurable, but not large enough to alter markedly the environment in the bottles. Preliminary experiments indicated that the rate of respiration in the bottles remained constant for at least 24 hr, and use of an entire day averaged any differences in the rate of photosynthesis arising from diurnal periodicities in the physiology of the plankton. The pairs of light bottles were located at depths where they received approximately 100, 50, 25, and 10% of the surface illumination. The depths were determined from the extinction coefficient of the water which was estimated from a Secchi disc measurement by use of the formula of

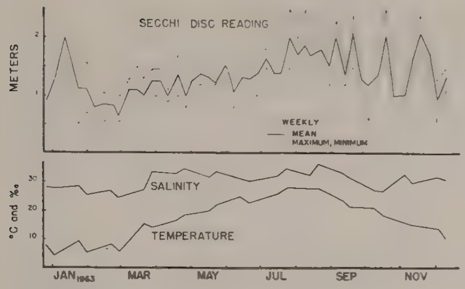

FIG. 1. Secchi disc reading, salinity, and water temperature.

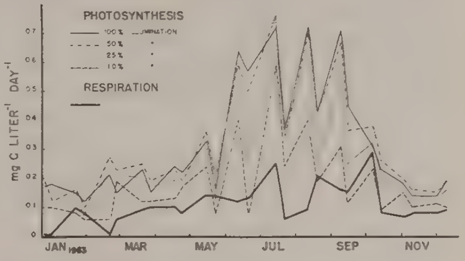

FIG. 2. Gross photosynthesis and respiration at four light levels.

Poole and Atkins (1929): extinction coefficient = 1.7/Secchi disc measurement in m.

The titration values for each group of duplicate or triplicate bottles were averaged and the group means were used to calculate changes in carbon. Replicates rarely differed by more than 0.13 mg O_2/liter (equivalent to 0.4 mg C/liter). This level of precision was similar to that reported by Patten et al. (1964) for the light- and dark-bottle method.

The abundance of algal cells and the concentration of chlorophyll *a* in material retained by HA Millipore®[2] filters were used to estimate standing crop of phytoplankton. Cell counts were made on freshly collected, unpreserved samples by examination of the filter after clearing with immersion oil. Chlorophyll *a* was extracted with 90% acetone and estimated with a Beckman model DU spectrophotometer following the method of Strickland and Parsons (1960). The optical densities obtained with the spectrophotometer were converted to pigment concentrations by means of nomograms (Duxbury and Yentsch 1956) representing the equations of Richards with Thompson (1952).

Measurements of insolation were obtained from two sources. A 50-junction Eppley pyrheliometer connected to a Varian G-10 recorder was in operation for 18 of the measurements. For the remaining eight measurements, radiation values were taken from data of the U.S. Weather Bureau (Climatological Date—National Summary) for Cape Hatteras—the station nearest Beaufort.

RESULTS

Physical data

Conditions in the Beaufort Channel are summarized in Fig. 1. Water temperature followed a seasonal cycle with a midwinter low of 4C and midsummer high of 28C. Salinity ranged from 24 to 36‰, with lowest values in the winter. The general pattern of alternately higher and lower salinities reflected the state of the tide when the sample was collected—higher salinities at high tide and lower salinities at low tide. Secchi disc readings ranged from 0.5 to 2.5 m and averaged 1.4 m. Extinction coefficients obtained from these ranged from 3.4 to 0.68 and averaged 1.2. The depth for the bottom of the euphotic zone (the level of 1% of surface illumination) obtained from this average coefficient was 4.6 m, indicating that the entire water column lay within the euphotic zone over most of the estuary most of the time. There were generally greater transparencies during summer and fall.

Productivity

Photosynthesis (Fig. 2) has a pronounced seasonal cycle with high values during the summer and early fall and low values throughout the remainder of the year. There was no suggestion of a spring bloom or other brief pulse of high production. The range for gross photosynthesis at the sur-

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[2] Registered trademark, Millipore Filter Corporation, Bedford, Massachusetts.

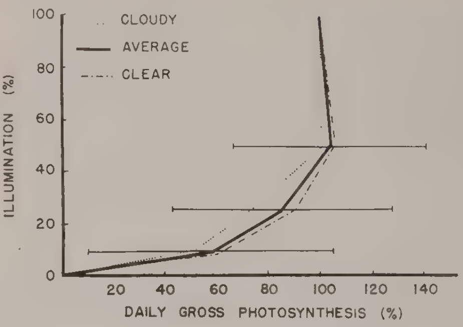

Fig. 3. Relative rates of photosynthesis at percentages of surface illumination. The lines indicate separate averages for clear and cloudy days, and an overall average. The horizontal bars indicate 95% confidence limits for the overall average.

face, 0.12 to 0.72 mg C liter^{-1} day ^{1}, was within that previously recorded for fertile inshore areas (Patten 1961; Riley 1941; Strickland 1960). The pattern of alternately higher and lower values for successive measurements was, like salinity, associated with the stage of the tide when the water was collected—high values with low-tide samples and low values with high-tide samples. This pattern indicated that the estuarine water was more productive than the ocean water. Differences in productivity between the estuarine and oceanic water were, as in the High Venice Lagoon (Vatova 1961), smaller in winter than in summer.

Throughout the year, maximum photosynthesis for the 24-hr day was obtained at either 100 or 50% of surface illumination; 25 and 10% illumination usually yielded successively lesser amounts (Fig. 2). These results agreed with a previous observation that a phytoplankton population exposed to changing illumination because of turbulent mixing, adapted to the higher levels of illumination (Ryther and Menzel 1959).

In each experiment, measurements of photosynthesis at 50, 25, and 10% of surface illumination were expressed as percentages of surface photosynthesis and these were pooled into a single curve (Fig. 3). Photosynthesis at these lower light intensities relative to photosynthesis at surface illumination varied widely between successive measurements and had no seasonal cycle. Average values ranged from 104% at 50% of surface illumination to 58% at 10% of surface illumination. Clear days produced relatively greater subsurface photosynthesis than cloudy days, but the differences were small, and except for the largest (that at 25% illumination) not significant (Fig. 3).

The relationships between insolation, water temperature, and surface gross photosynthesis are shown in Fig. 4. The similarity of the seasonal cycles in photosynthesis and temperature produced the obvious correlation between these variables. Measurements of photosynthesis formed two groups —high values obtained at 20C and above, and lower values obtained below 20C. The significant positive correlation between insolation and photosynthesis was, although not obviously, probably a reflection of the correlation between insolation and water temperature. Both measurements of photosynthesis at temperatures below 20C and measurements at 20C and above were made under a wide variety of light conditions (Fig. 4). When these groups of measurements were analyzed separately, the correlations between photosynthesis and insolation were no longer significant.

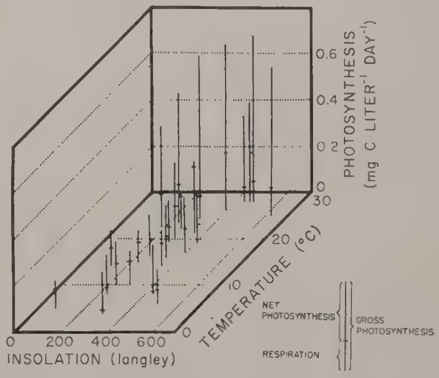

Fig. 4. Three-dimensional bar graph depicting daily rates of photosynthesis at surface illumination in relation to water temperature and to insolation. Each bar represents one measurement. The length of the bar indicates the photosynthesis obtained, and the location of the bar in the horizontal plane, the temperature and insolation during the experiment.

TABLE 1. *Summary of phytoplankton production data—average values*

	Chlorophyll *a* (μg/liter)	Secchi disc reading (m)		Gross Photosynthesis (mg C/day)	Respiration (mg C/day)
Low production period					
Dec–May and 14 Oct–Dec	4.8	1.14	At surface	$188/m^3$	$79/m^3$
			For a 1.0-m water column	$182/m^2$	$79/m^2$
			For a 4.0-m water column	$318/m^2$	$316/m^2$
High production period					
June–7 Oct	3.6	1.46	At surface	$547/m^3$	$162/m^3$
			For a 1.0-m water column	$553/m^2$	$162/m^2$
			For a 4.0-m water column	$1,196/m^2$	$648/m^2$

Estimated annual values for 125 high production and 240 low production days

	1.0 m water column	4.0 m water column
Gross photosynthesis (g C/m^2)	113	225
Respiration (g C/m^2)	39	157

Respiration, like photosynthesis, averaged higher in warm weather, but unlike photosynthesis, fluctuated irregularly from measurement to measurement (Fig. 2). Values ranged from 0.01 mg C liter^{-1}day^{-1} in midwinter to 0.29 mg C liter^{-1}day^{-1} in early October when the Beaufort Channel was conspicuously polluted with wastes from fish processing plants. Although respiration had a highly significant correlation with surface gross photosynthesis, the ratio of respiration to photosynthesis ranged from 5 to 93%. Under both warm and cool conditions (above and below 20C) respiration averaged approximately 40% of surface gross photosynthesis.

To estimate the rate of production in the estuarine system at Beaufort, gross photosynthesis and respiration were calculated for a water column 1.0 m deep (average depth of the Newport River estuary) and for a water column 4.0 m deep which included the entire euphotic zone (Table 1). Rates of subsurface photosynthesis were obtained by multiplying surface gross photosynthesis by the relative rates (Fig. 3) at 50, 25, and 10% of surface illumination. Below 10%, photosynthesis was assumed to be proportional to illumination. The light depths were estimated from the average Secchi disc reading. Integration of the rates of photosynthesis down to 1.0 or 4.0 m yielded photosynthesis/m^2. Data from the Beaufort Channel were divided between a warm, more productive period (June through 7 October) and the cool, less productive remainder of the year. These periods approximately corresponded to water temperatures above and below 20C.

The daily rates of gross photosynthesis/m^2 (Table 1) were similar to the range of values reported from coastal waters (Ryther 1963; Strickland 1960). The results suggest that photosynthesis was insufficient to support the respiration only in the deepest channels; elsewhere there was net photosynthesis.

In agreement with investigations elsewhere (Yentsch and Ryther 1959), phytoplankton production throughout the year in the Beaufort Channel was derived preeminently from the nannoplankton (Fig. 5). Removal of net plankton decreased surface gross photosynthesis an average of 27% between June and 7 October, and 9% the remainder of the year. Results were similar at the three lower levels of illumination. Respiration, however, was increased an average of 17% by removal of net plankton. In many cases the increase seemed too large to have resulted from errors in technique. The in-

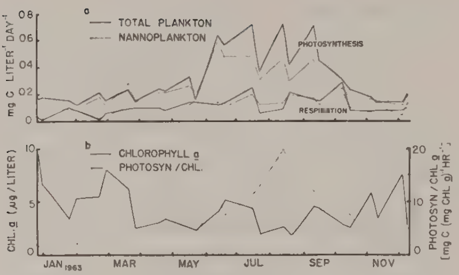

FIG. 5. *a.* Gross photosynthesis at surface illumination and respiration of total plankton and of nannoplankton alone. *b.* Chlorophyll *a* concentration and the ratio of the average rate of gross photosynthesis during the daylight hours at surface illumination to chlorophyll *a* concentration.

crease in the filtered water might have resulted from increased bacterial activity following the removal of algae or other material releasing antibiotics.

Standing crop

There was no seasonal change in cell numbers corresponding to the cycle in productivity. Cell counts varied irregularly from 0.13 to 5.4×10^6 cells/liter, but averaged 2×10^6 in both warm and cool weather. Although flagellates often were present, small centric diatoms, such as *Skeletonema costatum,* were the most abundant plankton throughout the year. Filtration of the water through No. 25 netting reduced both cell numbers and chlorophyll *a* concentration an average of 21%.

The seasonal cycle of chlorophyll *a* concentration suggested an inverse relationship between chlorophyll *a* and gross photosynthesis (Fig. 5), because the average concentration was 4.8 μg/liter during the cool, less productive period and 3.6 μg/liter during the warm, more productive period (Table 1). The range in chlorophyll *a* concentration in the Beaufort Channel, 2.0 to 9.3 μg/liter (Fig. 5), was similar to that observed in Chesapeake Bay (Patten et al. 1963) and Long Island Sound (Conover 1956) except during phytoplankton blooms in those localities. However, chlorophyll *a* estimates may at times have included significant amounts of detrital pigment and thus may not precisely delineate the seasonal cycle in phytoplankton pigment. A highly significant positive correlation between chlorophyll *a* concentrations and Secchi disc readings suggested that part of the pigment in the higher concentrations was derived from material temporarily suspended at times of reduced transparency, and a lack of significant correlation between Secchi disc readings and surface gross photosynthesis suggested that this material was detrital.

Relationship between chlorophyll and photosynthesis

The seasonal variation in surface gross photosynthesis and its negative correlation with chlorophyll *a* were reflected in the pronounced seasonal cycle in the rate of photosynthesis per unit of chlorophyll *a* (Fig. 5). The values were obtained by dividing gross photosynthesis over the 24-hr day by the concentration of chlorophyll and by the period of daylight (9.8 to 14.4 hr). Values ranged from 1.9 mg C(mg Chl a)$^{-1}$ hr^{-1} in early winter to 19.8 in midsummer. The average for the more productive period was 12.1 mg C(mg Chl a)$^{-1}$ hr^{-1}, and for the less productive period, 4.2. The ratios of photosynthesis to chlorophyll, although higher than many of those previously reported, were minimal estimates of the ratio potentially obtainable at optimum illumination, because insolation approximated the optimum level only briefly during the experiments.

There was no significant correlation between average intensity of insolation and the ratio of photosynthesis to chlorophyll, and the position of the seasonal cycle in this ratio (Fig. 5) suggested that its value was a function of water temperature rather than of insolation. The relationship between the logarithm of the ratio and temperature (Fig. 6) was fitted to a least squares regression:

$$\log [\text{mg C}(\text{mg Chl } a)^{-1}\ \text{hr}^{-1}] = 0.138 + 0.0353 \times \text{temperature } (^\circ\text{C}).$$

The slope of the regression yielded a Q_{10} value of 2.25 for the ratio; 95% confidence limits were 1.86 and 2.73. Values predicted by the regression for individual measurements should, in 95% of the cases, lie between one-half and twice the true value (Fig. 6). Secchi disc readings for the observations above the regression line averaged 1.4 m and for those below the line 1.0 m, suggesting that some of the scatter arose from variations in the ratio of phytoplankton pigment to detrital pigment.

DISCUSSION

Although temperature, salinity, and transparency in the Beaufort Channel appear to be suitable for the growth of phytoplankton throughout the year, there is a pronounced seasonal cycle in phytoplankton production that tends to follow the water temperature cycle. Annual cycles in the production of marine phytoplankton, with higher values in summer, are characteristic of shallow temperate embayments. Such cycles have been observed in widely separated studies—Long Island Sound and bays along the coasts of Massachusetts, Italy, and Denmark. They have been ascribed to a more rapid regeneration of nutrients in warm weather following increased bacterial metabolism at elevated temperatures (Grøntved 1960; Riley 1941, 1956; Ryther 1963; Steemann Nielsen 1958; Vatova 1961). The mechanism of this temperature regulation in the Beaufort Channel is unknown, but it may be related to the rate of nutrient regeneration.

The seasonal and short term variations in the phytoplankton production in the Beaufort Channel are intermediate in magnitude among those reported in previous inshore studies. Seasonal variation was small in Long Island Sound (Riley 1941), threefold in the Beaufort Channel and 10- to 20-fold in the Danish Belt (Steemann Nielsen 1958) and in the High Venice Lagoon (Vatova 1961), although the seasonal variation in water temperature was greater in the Beaufort Channel and Long Island Sound than in the Venice Lagoon and the Danish Belt. Short term variations were negligible in the High Venice Lagoon (where each estimate of daily production is an average of a high and a low tide sample), two- to fourfold in the Beaufort Channel and the Danish bays, and up to ninefold in Long Island Sound. Had the estimate for the High Venice Lagoon been based on alternate high tide and low tide samples, short term variations there would have been twofold and thus similar to those at Beaufort. These four studies suggest that the amplitude of the seasonal cycle in phytoplankton production is not closely related to seasonal variation in water temperature and that short term variations in phytoplankton production are least in areas like the High Venice Lagoon and the Beaufort Channel where tidal exchanges are large. The pattern of respiration in the Beaufort Channel is similar to that in Long Island Sound (Riley 1941) with an average value close to half the gross production, much irregular variation, and higher rates in warm weather.

Although the rate of gross photosynthesis per unit volume is moderately high near the surface in the Beaufort Channel (that is, three times that of Long Island Sound) this

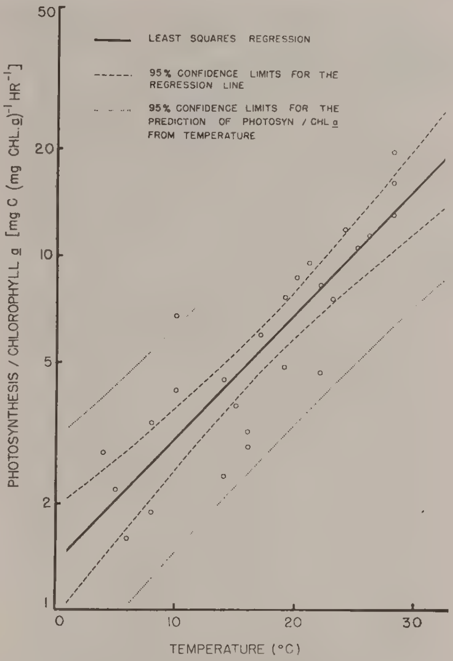

FIG. 6. The effect of water temperature on the ratio of the rate of gross photosynthesis to chlorophyll *a* concentration.

rate is insufficient to compensate for the shallowness and turbidity of the water, so photosynthesis per unit area is no greater than that in many regions of the open sea and far below that of fertile benthic communities of marsh grass or macroscopic algae (Odum 1961; Riley 1941; Ryther 1963). Although reduction in turbidity would markedly increase photosynthesis per unit area in the deeper channels, such channels comprise only a small fraction of the Newport River estuary. Much of the estuary is so shallow that light adequate for rapid photosynthesis already penetrates to the bottom. In these areas, production per unit area could be markedly elevated only by increasing the rate of production per unit volume.

The daily rate of surface photosynthesis in the Beaufort Channel can be predicted from chlorophyll *a* concentration, day length, and water temperature by a three-step procedure: 1) Obtain the ratio of photosynthesis to chlorophyll *a* from water temperature (Fig. 6). 2) Obtain the mean hourly rate of photosynthesis by multiplying this ratio by the concentration of chlorophyll *a*. 3) Multiply the mean hourly rate by the hours of daylight. The procedure differs from that of Ryther and Yentsch (1957) principally in that a variable ratio of photosynthesis to chlorophyll is substituted for their single fixed value, and in that the rate of photosynthesis is expressed as the mean rate at the surface during daylight hours rather than the rate occurring at optimal illumination. Adjusting the ratio of photosynthesis to chlorophyll *a* for changes in temperature increases the accuracy of prediction. Daily rates calculated by this three-step procedure differed from the measured rates (Fig. 2) by an average of 26%, whereas daily rates calculated from a constant ratio of photosynthesis to chlorophyll *a* [the mean for the 26 samples: 6.9 mg C (mg Chl $a)^{-1}$ hr^{-1}] differed from the measured rates by an average of 58%. Use of the mean rate for photosynthesis during daylight hours avoids the need for first measuring the rate at various light intensities and subsequently calculating rates at different times of day from these measurements.

An increase in the ratio of photosynthesis to chlorophyll with increasing temperature is present in the data of Barlow, Lorenzen, and Myren (1963), Hepher (1962), Ichimura (1960), Steemann Nielsen and Hansen (1961), and Ryther and Yentsch (1957), suggesting that it is a widespread phenomenon, at least in locations where photosynthesis is not limited by a shortage of nutrients. Observations on the temperature dependence of the rate of light-saturated photosynthesis (Ichimura 1960; Talling 1957; Wassink et al. 1938) provide a possible explanation for this increase in assimilation numbers with increasing temperature. These studies on planktonic algae indicated that once a certain light intensity is reached, the speed of the dark reactions limits the rate of photosynthesis. With constant temperature, further increases in illumination above this point of light saturation do not increase photosynthesis. However, the dark reactions are speeded by increased temperature, elevating the light intensity at which saturation occurs, and permitting more complete utilization of the light energy. The average Q_{10} value for light-saturated photosynthesis in these three studies lay between 2.3 and 2.5, values close to the Q_{10} of the ratio of photosynthesis to chlorophyll *a* for phytoplankton at the surface of the Beaufort Channel. Since it is likely that the photosynthesis of phytoplankton exposed to surface illumination is not light limited throughout much of the day, it is reasonable to find the rate of photosynthesis modified by temperature.

Values far in excess of 3.7 mg C(mg Chl $a)^{-1}$ hr^{-1} for photosynthesis per unit of chlorophyll obtained in warm weather may not be artifacts arising from incomplete extraction of pigment, as suggested by Barlow et al. (1963) and by Ryther and Yentsch (1957). In our study, underestimation of this ratio through overestimation of phytoplankton chlorophyll seems more probable because of contamination by detrital pigments. Diatoms, the dominant algal group observed in the cell counts, are completely extracted by 90% acetone (Antia et al. 1963). Although an abundance of small plankters, inconspicuous on a cleared Millipore filter and incompletely extracted by 90% acetone, is not impossible, our data contain no evidence of such organisms. An alternative explanation for the high values observed in warm weather in the surface layers of stratified waters (Ichimura 1960) as well as in shallow, fertile embayments is that they truly represent the physiological condition of the phytoplankton.

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LIPID-SOLUBLE PIGMENTS, VITAMINS, AND PROSTAGLANDINS

I. PIGMENTS

Carotenoids. Representatives of this class of non-saponifiable lipids are found in small amounts in all higher plants, in many microorganisms, and probably in all animals. These pigments, composed basically of eight isoprenoid units linked symmetrically about the center of the molecule, contain a chromophoric system of conjugated carbon-carbon double bonds. Although *de novo* synthesis of carotenoids occurs only in plants, both plants and animals effect molecular interconversions among carotenoids. Carotenoid biosynthesis closely parallels steroid synthesis to the formation of geranylgeranyl pyrophosphate, but the C-40 analogue of squalene, lycopersene, has not been demonstrated. Instead, the first detectable C-40 compound is phytoene, which undergoes subsequent stepwise dehydrogenation to lycopene.[1-5]

Most carotenoids may be considered derivatives of the red pigment lycopene, which undergoes structural modification by terminal ring closure to an analogue of either α-ionone (α-carotene) or β-ionone (β-carotene), by introduction of oxygen (epoxy, hydroxy, or carbonyl) into the molecule (xanthophylls), or by oxidative cleavage of the carbon-carbon chain (apo-carotenoids, such as azafrin). Cis isomers of carotenoids are designated by the prefix *neo-* and a letter indicating the specific isomer.[6] The numbering system, shown in Figure 1 for lycopene, and the nomenclature regarding carotenoids have been assigned with general agreement in the U. S.[7] and in Europe.[8]

Extraction and saponification of carotenoids are generally performed in dim light and under an inert atmosphere to prevent light-catalyzed reactions and oxidation of the pigments. Complete extraction of carotenoids is facilitated if the tissue is dried initially by grinding with anhydrous sodium sulfate,[9-11] or by repetitive extraction with anyhdrous acetone, ethanol or methanol.[12-15] Pigments are usually transferred to petroleum ether and the solution is dried if necessary before further study.

Hydrocarbon carotenoids and xanthophylls containing one hydroxyl or two carbonyl groups are generally soluble in a wide range of solvents, in-

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By Douglas A. Wolfe, U.S. Bureau of Commercial Fisheries, Beaufort, North Carolina. Reprinted from The Handbook of Biochemistry and Physics (Henry C. Damm, editor), The World Publishing Company, Cleveland and New York, xv + 736 p.

cluding carbon disulfide, benzene, chloroform, acetone, ether and petroleum ether, and are also slightly soluble in ethanol and methanol. As the degree of oxygenation increases, the solubility in petroleum ether, ether, etc., diminishes with corresponding increases in solubility in the alcohols. Acidic carotenoids, such as astaxanthin, bixin and crocetin, are very soluble in pyridine and slightly soluble in dilute alkaline solutions. All other carotenoids are insoluble in water. The technique of separating complex mixtures of carotenoids by partitioning them between two immiscible solvents has been extensively used.[16, 17] When partitioned in a petroleum ether-95% methanol system, hydrocarbon carotenoids distribute exclusively in the epiphase, and diol carotenoids distribute largely in the hypophase. Only recently, however, have quantitative partition coefficients been reported for use in the analytical characterization of carotenoids.[9, 18-29]

Chromatography of carotenoids is most frequently performed on columns of alumina, calcium hydroxide, calcium carbonate or zinc carbonate.[16] Petroleum ether, alone or mixed with benzene, ether or acetone, is commonly used as an eluant for carotenes. For more polar carotenoids, benzene-ether, ether, or acetone is used. Methods for the isolation and analysis of β-carotene are thoroughly described by Bickoff.[245] Absorption of visible and ultra-violet light is most extensively used in the characterization of carotenoids,[30] but this has been supplemented by infra-red absorption[31-35] and nuclear magnetic resonance and proton resonance studies.[31, 32, 36] Ketocarotenoids have been examined spectrophotometrically before and after reduction by sodium borohydride.[9] Carotenoid 5-6 epoxides can be identified by a spectral shift toward shorter wavelengths when treated in ethanolic solution with a trace of HCl.[9, 16] Finally, thin-layer chromatography has been applied to carotenoid studies.[37-42] The following table draws heavily from the review of Karrer and Jucker.[16] For a more comprehensive coverage of the chemistry and biochemistry of carotenoids, see this and other reviews.[5, 43, 44]

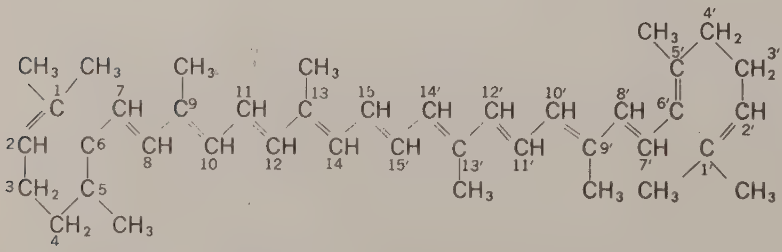
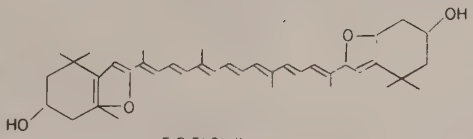
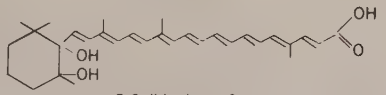
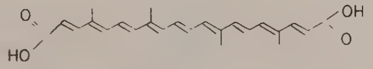


Figure 1. Structure and numbering of Lycopene.

Table I. Properties of Carotenoids (References are shown in brackets)

No.	Carotenoid	Formula	M. wt.	Crystallization	M.P.	Absorption Maxima	Part Coeff.	Occurrence
1	Antheraxanthin	5:6 epoxy-zeaxanthin $C_{40}H_{56}O_3$	584.85	needles or thin platelets from MeOH or benz-MeOH	205 [45]	CS_2 510 478 $CHCl_3$ 490.5 460.5	4/96 (p.e./85) [9] 39/61(p.e./70)	anthers of Lilium trigrinum [45, 46] berries of Euonymus europaeus [47] flower of Delonix regia [28] Euglena gracilis [9]
2	Aphanin	see Echinenone [43, 48, 49]	–	–	–	–	–	–
3	Aphanizophyll	see Myxoxanthophyll ? [43, 50, 51]	–	–	–	–	–	–
4	Astacene	3,3′,4,4′ tetra-keto β-carotene $C_{40}H_{48}O_4$	592.78	violet needles from pyr.-H_2O	228 [52]	CS_2 500 hexane 470	–	not naturally occurring, but readily formed from astaxanthin [52, 53]
5	Astaxanthin	3,3′ di-hydroxy, 4.4′ di-keto β-carotene $C_{40}H_{52}O_4$	596.82	platelets from pyr.	215–216d [16]	CS_2 502 hexane 466–467	–	protein complexes in Crustacea [53–56]; Crustacea [43, 57]; Echinoderms [58–60]; Fish [61, 62]; Birds [52, 63, 64]; green algae [65]
6	Auroxanthin	 5:8,5′:8′-diepoxy-zeaxanthin $C_{40}H_{56}O_4$	600.85	yellow needles from MeOH	203	CS_2 454 423 EtOH 428 402 382	50/50 (p.e./66.7) [29]	flowers of Viola tricolor [66]
7	Azafrin	 5,6-di-hydroxy-β-apo-10′-carotenoic acid $C_{27}H_{38}O_4$	426.85	redorange needles from benz; prisms from toluene	212–214	$CHCl_3$ 458 428 pyr. 458 428 aq. NaOH 447 422	–	Escobedia scabrifolia; Escobedia linearis [67]
8	Bixin	 $C_{25}H_{30}O_4$	394.99	violet dichroic prisms from acetic acid	191.5	CS_2 523.5 489 457 $CHCl_3$ 503 469.5 439	–	Bixa orellana [68]

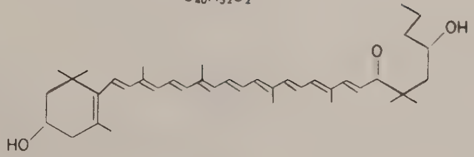
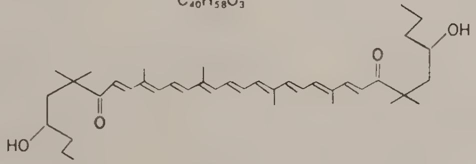
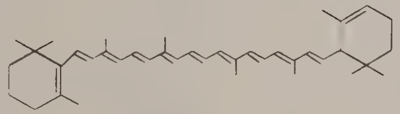
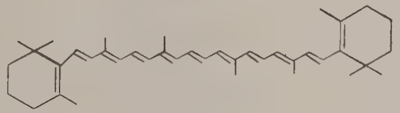
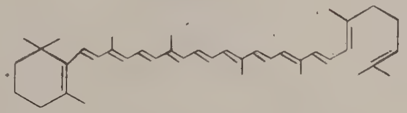
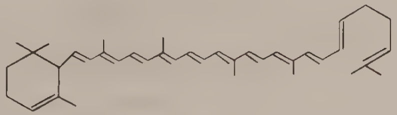
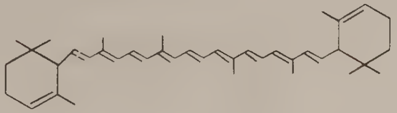
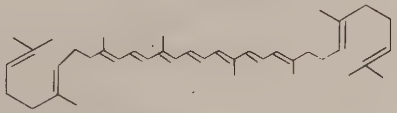
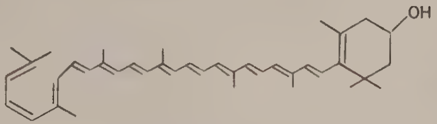
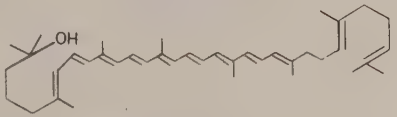
9	Canthaxanthin	4,4′-diketo-β-carotene $C_{40}H_{52}O_2$	564.82	platelets from benz.-MeOH	204 [69]	benz. hexane pet. eth.	480 466 462–3	50/50 (hex/95)	Mushroom, Cantharellus cinnabarinus [70]; birds [69, 71–74]; Crustacea [75, 76]; insects [77]
10	Capsanthin	 $C_{40}H_{58}O_3$	586.86	red needles from pet. eth.; prisms from MeOH	175–176 [46, 78]	CS_2 benz. pet. eth.	542 503 520 486 505 475	4/96 (hex/95)	Lillium tigrinum [46]; Capsicum annuum [79]
11	Capsorubin	 $C_{40}H_{60}O_4$	604.88	violet-red needles from benz.-pet. eth.; rhombic plates from CS_2	201	CS_2 benz. pet. eth.	541.5 503 468 520 486 455 506 474 444	1/99 (hex/95)	Capsicum annuum [80, 81]
12	α-Carotene	 $C_{40}H_{56}$	536.85	violet prisms from benz.-MeOH	187–188 [82]	CS_2 $CHCl_3$ hexane pet. eth.	509 477 485 454 475 445 420 [395] 478 447.5	100/0 (hex/95)	Plant tissues generally [16]
13	β-Carotene	 $C_{40}H_{56}$	536.85	violet hexagonal prisms from benz. MeOH; red plates from pet. eth.	183 [83]	CS_2 $CHCl_2$ hexane pet. eth.	520 485 450 497 466 477 450 425 483.5 452 426	100/0 (hex/95)	Plant and animal tissues generally [16]
14	γ-Carotene	 $C_{40}H_{56}$	536.85	red prisms from benz.-MeOH	178 [84] 176.5 [85]	CS_2 benz. $CHCl_3$ hexane pet. eth.	533.5 496 463 510 477 447 508.5 475 446 494 462 431 495 462 431	100/0 (hex/95)	Traces in many plant tissues [16, 84]

Table I. Properties of Carotenoids (References are shown in brackets) (cont'd)

No.	Carotenoid	Formula	M. wt.	Crystallization	M.P.	Absorption Maxima	Part Coeff.	Occurrence
15	δ-Carotene	 $C_{40}H_{o}$ [89]	536.85	yellow-orange crystals from benz.-MeOH	140.5 [199]	hexane 485 456 430	—	Traces in many plant tissues Tomatoes [86] Bacteria [87, 88]
16	ε-Carotene	 $C_{40}H_{56}$	536.85	yellow-red leaflets from benz.-MeOH	190 [90]	hexane 469 439 415 benz. 482 451 425	—	Marine diatoms and algae: Bryopsis, Navicula, Cryptomonas [91, 92]
17	ζ-Carotene	 $C_{40}H_{60}$	540.88	—	—	hexane 424 399 377	100/0 (hex/95)	Traces in many plant tissues; Carica papaya [93]
18	Celaxanthin	 $C_{40}H_{54-56}O$?	550.83 552.85?	long needles from pet. eth.-EtOH	209–210	CS_2 562 521 487 455 EtOH 520.5 488 455 pet. eth. 520 486.5 456 [429]	—	Celastrus scandens [94]
19	Chloroxanthin	 $C_{40}H_{60}O$	556.88	needles from pet. eth.	139 [23]	pet. eth. 468 437.5 413	90/10 (p.e./95)	Rhodopseudomonas spheroides [23] [96]
20	Chrysanthemaxanthin	Cis-trans isomer of flavoxanthin [43]	—	—	—	—	—	

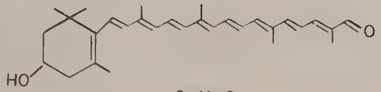
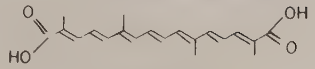
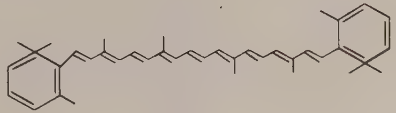
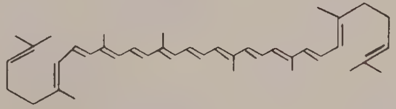
21	β-Citraurin	 $C_{30}H_{40}O_2$	432.62	yellow plates from benz.-petrol	147	CS_2 benz. hexane	525 490 457 497 467 487 458		orange peels (Citrus aurantium) [97, 98]
22	Citroxanthin	see Mutatochrome							
23	Crocetin	 $C_{20}H_{24}O_4$	328.39	red rhombs from acetic anhydride	285	CS_2 pyr. $CHCl_3$ pet. eth. hexane	482 453 426 464 436 411 463 434.5 450.5 424.5 445 420 400	4/96 (hex/95)	Crocus species and other flowers and fruits [99]
24	Cryptoxanthin	3-hydroxy-β-carotene $C_{40}H_{56}O$	552.85	prisms from benz.-MeOH	169	CS_2 $CHCl_3$ EtOH hexane	519 483 452 497 463 433 486 452 424 484 451 423	82/18 (hex/95) [18] 77/23 (p.e./95) [9]	several plants, incl. Physalis species [100]; Crustacea [101, 102]; chicken eyes [103]; egg yolks [104]; butter [105]
25	Echinenone	4-keto-β-carotene $C_{40}H_{54}O$	550.83	violet needles from benz.-MeOH or pet. eth.	178–179	CS_2 pet. eth.	488 458	93/7 (hex/95)	echinoderms [106, 107]; Crustacea [75]; Euglena gracilis [9]
26	Eloxanthin	5:6-epoxy-lutein $C_{40}H_{56}O_3$	584.85	red-yellow crystals from benz.-MeOH	192 [108]	CS_2 benz. EtOH pet. eth.	501.5 472 482 453 473 445 471 442	—	leaves and flowers of various plants [16], incl. Elodea canadensis [109]
27	Eschscholtzxanthin	— $C_{40}H_{54}O$? [110, 111]	566.83	from acetone or ether	185–186	CS_2 benz. EtOH $CHCl_3$ pyr.	536 502 475 516 485 458 503 472 446 513 484 456 521 489 463	—	Eschscholtzia californica [112]
28	Euglenanone	3,4-diketo-β-carotene? $C_{40}H_{52}O$?	564.82	—	—	$CHCl_3$ EtOH pet. eth.	478–482 473 458	44/56 (p.e./95)	Euglena gracilis [9]
29	Flavacin	?see ζ-carotene [43]	—	—	—		—	—	—
30	Flavochrome	5:8-epoxy-α-carotene $C_{40}H_{56}O$	552.85	yellow plates from benz.-MeOH	189	CS_2 benz. $CHCl_3$ pet. eth.	482 451 462 434 461 433 450 422	—	Ranunculus acer [113] Tragopogon pratensis [113]
31	Flavorhodin	?see ε-carotene [43]	—	—	—		—	—	

Table I. Properties of Carotenoids (References are shown in brackets) (cont'd)

No.	Carotenoid	Formula	M. wt.	Crystallization	M.P.	Absorption Maxima	Part Coeff.	Occurrence
32	Flavoxanthin	5:8-epoxy-lutein $C_{40}H_{56}O_3$	584.85	yellow prisms from MeOH	184	CS_2 479 449 $CHCl_3$ 459 430 EtOH 448 421 pet. eth. 450 421	—	many plant tissues [16]; incl. dandelion [114], Ranunculus acer [115]
33	Fucoxanthin	? $C_{40}H_{56-60}O_6$	—	red needles from eth.-pet., eth.	159.5–160.5 [116]; 166–168 [117]	CS_2 510 477 445 $CHCl_3$ 492 457 hexane 469 451 438	2/98 (p.e./85) [21] 72/28 (p.e./60)	brown algae, incl. Fucus, Dictyota, Cystosira, and Laminaria [118]
34	Galloxanthin	—	—	—	—	CS_2 446 424 — $CHCl_3$ 427 407 [387] EtOH 421 400 378 hexane 422 401 [380]	hypophasic (p.e./90)	chicken retina [119]
35	Gazaniaxanthin	? $C_{40}H_{54-58}O$	—	red plates from benz.-MeOH	133–134	CS_2 531 494.5 461 benz. 509 476 447.5 EtOH 494.5 462 434.5 pet. eth. 494.5 462.5 434.5	80/20 (hex/95)	Gazania rigens [120]
36	Leprotene	 $C_{40}H_{48}$ [329]	528.78	—	198–200 [328] 189–192 [329]	pet. eth. (428) 452 480 acetone (435) 458 485 benz. (440) 465 494 CS_2 (460) 484 515	—	Mycobacterium species [329]
37	Lutein	3,3′-dihydroxy-α-carotene $C_{40}H_{56}O_2$	584.85	violet prisms from MeOH	193 [120]	CS_2 508 475 445 $CHCl_3$ 487 456 428 EtOH 476 446.5 420 hexane 477 447 420	12/88 (hex/95) 43/57 (hex/85) 50/50 (hex/82.3)	Widely distributed in green plants; leaves, flowers, fruits, and seeds; also from many animal tissues [16]
38	Lycopene	 $C_{40}H_{56}$	536.85	red needles from CS_2-EtOH	174 [121] 175 [122]	CS_2 548 507.5 477 $CHCl_3$ 517 480 453 benz. 522 487 455 EtOH 503 472 443 hexane 504 472 443	100/0 (hex/95)	fruits and seeds, e.g., tomatoes; green plants; some animal tissues [16]

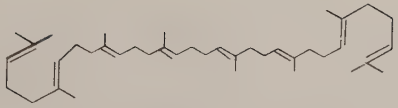
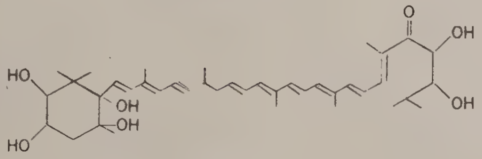
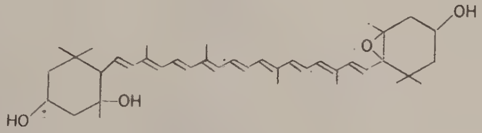
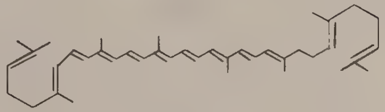
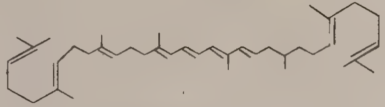
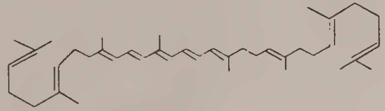
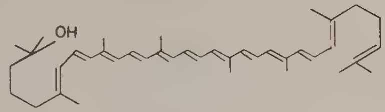
39	Lycopersene	 $C_{40}H_{66}$	546.93	colorless oil	octa-HCl: 126 [336]		—	—	not occurring naturally in carotenoid-biosynthetic organisms [2]
40	Lycophyll	3,3′-dihydroxy-lycopene $C_{40}H_{56}O_2$	568.85	violet leaflets from benz.-MeOH; red needles from benz.-pet. eth.	179	CS_2 benz. EtOH pet. eth.	546 506 472 521 487 456 505 474 444 504 473 444	—	Solanum dulcamara, Solanum esculentum [123]
41	Lycoxanthin	3-hydroxy-lycopene $C_{40}H_{56}O$	552.85	red-brown plates from benz.-pet. eth.; violet needles from CS_2	168	CS_2 benz. EtOH pet. eth.	546 506 472 521 487 456 505 474 444 504 473 444	—	S. dulcamara; S. esculentum [123]
42	Mutatochrome	5:8-epoxy-β-carotene $C_{40}H_{56}O$	552.85	yellow-orange leaflets from benz.-MeOH	163–164 [124]	CS_2 benz. $CHCl_3$ pet. eth.	489.5 459 470 440 469 438 456 427	98/2 (hex/95) [28]	orange peels [125]
43	Myxoxanthin	see Echinenone [43, 48, 49]	—	—	—		—	—	—
44	Myxoxantho-phyll	 ?[126] $C_{40}H_{56}O_7$	648.85	violet needles from acetone	182 [126]	pyr. $CHCl_3$ EtOH	526 489 458 518 484 454 503 471 445	—	Oscillatoria rubescens [126, 127]
45	Neoxanthin	 ?[128, 133] $C_{40}H_{58}O_4$	602.86	—	—	$CHCl_3$ EtOH	475 445 421 466 437–8 413–4 (390)	0/100 (p.e./70) 8/92 (p.e./60) 37/63 (p.e./50)	leaves of green plants [129] Euglena gracilis [9, 128] [130]

Table I. Properties of Carotenoids (References are shown in brackets) (cont'd)

No.	Carotenoid	Formula	M. wt.	Crystallization	M.P.	Absorption Maxima	Part Coeff.	Occurrence
46	Neurosporene	 $C_{40}H_{58}$	538.87	crystals from EtOH	117 [23]	pet. eth. 468 437.5 413	100/0 (p.e./95)	Neurospora crassa and other fungi [43, 131] Rhodopseudomonas spheroides [23] [96]
47	Neurosporoxanthin	(acidic carotenoid)?	—	purple leaflets from hexane	192 [132]	hexane 472 benzene 486	—	Neurospora crassa [132, 133] Fusarium aquaeductuum
48	Petaloxanthin	?cis-trans isomer of antheraxanthin [16, 43]	—	—	—	—	—	—
49	Phytoene	 $C_{40}H_{64}$	544.91	colorless oil	—	hexane 298 286 275	100/0 (hex/95)	trace amounts widely distributed in plants [134, 135]
50	Phytofluene	 $C_{40}H_{62}$	542.89	colorless oil	—	pet. eth. 367–8 348 332	100/0 (hex/95)	trace amounts widely distributed in plants [136, 137]
51	Rhodopin	 $C_{40}H_{58}O$	554.86	from acetone-pet. ether	172–174 [31]	pet. eth. 504 472 445 acetone 504 472 445	76/24 (p.e./95)	photosynthetic green bacteria, incl. Chloropseudomonas ethylicus, Chlorobium thiosulfatophilum, Chlorobium limicola, Rhodomicrobium vannielii [31, 32]

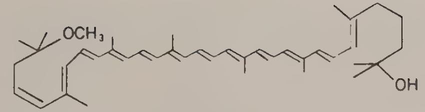
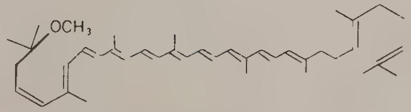
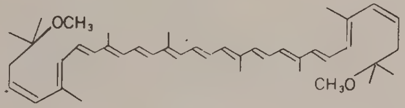
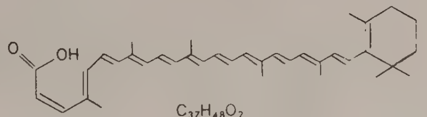
52	Rhodovibrin	 $C_{41}H_{60}O_2$	584.89	red crystals from CS_2-pet. ether	168 [138]	CS_2 acetone	556 517 521 488 460	66/34 (p.e./95) [24] 95/5 (p.e./85)	Rhodovibrio bacteria [138] Rhodomicrobium vannielii [31]
53	Rhodoviolascin	see spirilloxanthin	—	—	—	—	—	—	—
54	Rhodoxanthin	3,3′-diketo-dehydro-β-carotene $C_{40}H_{50}O_2$	562.80	violet needles from benz.-MeOH	219	CS_2 $CHCl_3$ benz. EtOH hexane	564 525 491 546 510 482 542 503.5 474 538 496 524 489 458	—	widely distributed in plants, incl. Taxus baccata [139]
55	Rubixanthin	3-hydroxy-γ-carotene $C_{40}H_{56}O$	552.85	orange-red needles from benz.-pet. ether	160	CS_2 $CHCl_3$ EtOH hexane	533 494 461 509 474 439 496 463 433 494 462 432	82/18 (hex/95) [28]	Cuscuta salina, Cuscuta subinclusa [140]; Rosa species [141, 142]
56	Sarcinaxanthin	?	—	red spheroids from benz.-petrol	149-150	CS_2 $CHCl_3$ benz. EtOH	499 466.5 436 480 451 423 481 451 424 469.5 441 [415]	—	Sarcina lutea [143]
57	Spheroidene	 $C_{41}H_{60}O$ [96]	568.89	yellow needles from pet. eth.	145 [23]	CS_2 $CHCl_3$ benz. pet. eth.	518 485 458 497 465 437.5 498 466 438 484 452 426.5	—	Rhodopseudomonas spheroides [23, 330]
58	Spheroidenone	2-keto-spheroidene $C_{41}H_{58}O_2$ [96]	582.87	red platelets from pet. eth.	163 [23]	CS_2 $CHCl_3$ benz. pet. eth.	553 519.5 495 499 530 499 475 513 482 460	—	Rhodopseudomonas spheroides [23, 330]
59	Spirilloxanthin	 $C_{42}H_{60}O_2$	596.90	red spindles from benz.	218	CS_2 benz. $CHCl_3$ EtOH	573.5 534 496 548 511 482 544 507 476 526 491 [465]	88/14 (p.e./95) [26]	rhodovibrio and thiocystis bacteria [144, 145]

Table I. Properties of Carotenoids (References are shown in brackets) (cont'd)

No.	Carotenoid	Formula	M. wt.	Crystallization	M.P.	Absorption Maxima	Part Coeff.	Occurrence
60	Taraxanthin	? $C_{40}H_{56}O_4$	600.85	prisms or plates from MeOH	184–185 [146]	CS_2 501 469 441 petrol 472 443	—	dandelion (Taraxacum officinale) [147–149]
61	Torularhodin	 $C_{37}H_{48}O_2$	474.75	red needles from MeOH-eth.	201–203d	CS_2 582 541 502 benz. 557 519 485 pyr. 558 518 485 $CHCl_3$ 554 515 [483] EtOH 532 495 463	—	Torula rubra [150, 151] [152]
62	Torulin	?	—	from benz.-MeOH	185	CS_2 565 525 491 pyr. 545 508 475 benz. 541 503 470 $CHCl_3$ 539 501 469 EtOH 520 486 456	—	Torula rubra, Sporobolomyces species Lycogala epidendron [152, 153]
63	Trollixanthin	(mono-epoxy-tri-hydroxy) ? $C_{40}H_{56}O_4$	600.85	yellow leaflets from benz.	199	CS_2 501 473 benz. 483 457 $CHCl_3$ 482 455 EtOH 474 447	—	Trollius europaeus [154, 155]
64	Violaxanthin	5:6,5′:6′-diepoxy-zeaxanthin $C_{40}H_{56}O_4$	600.85	yellow-orange prisms from MeOH	200	CS_2 501 470 440 $CHCl_3$ 482 451.5 424 EtOH 471.5 442.5 417.5 MeOH 469 440 415	50/50 (p.e./66.2) [29]	widely distributed in flowers and fruits [16]; incl. Viola tricolor (pansy) [156–168]
65	Zeaxanthin	3,3′-dihydroxy-β-carotene $C_{40}H_{56}O_2$	568.85	yellow plates from MeOH	215.5 [159]	CS_2 517 482 450 $CHCl_3$ 495 462 429 EtOH 483 451 423.5 MeOH 480.5 449.5 421.5	11/89 (hex/95) 40/60 (hex/85)	widely distributed in plants [16], incl. Zea mays [160]; egg yolk [161]; human fat [162]

[a] Additional spectral data are presented in references [30, 327].

[b] Partition coefficients are presented as the ratio of the epiphasic to hypophasic carotenoid, with the phasic system described in parentheses. (p.e. = petroleum ether; hex = hexane; 95 = 95% methanol; 90 = 90% methanol, etc.) Additional data are available from references [18, 29].

Chromolipids. This class of pigments, which gives rise to the yellow to brown coloration frequently observed in the adipose tissues of animals, is very poorly defined chemically. In addition, confusion exists in the literature because the term lipochrome is variously used as a synonym for both chromolipid and carotenoid. Chromolipids are generally regarded as complex mixtures of oxidation products of fatty acids or phospholipids, but, although they are probably produced metabolically, the function and fate of these pigments are not known.[163] Histochemical staining methods are frequently used in the study of chromolipids,[164–166] and, *in vitro,* autoxidation products of unsaturated lipids give the same reactions as cellular chromolipids.[165] Chromolipids exhibit absorption in both the ultraviolet and visible regions of the spectrum,[167] but can be differentiated from carotenoids by the absence of absorption bands in the blue-green region.[163]

II. FAT-SOLUBLE VITAMINS

Vitamin A. Carotenoids containing an unsubstituted β-ionine ring are converted in certain animal tissues to vitamn A or retinol. The conversion to retinol$_1$ occurs in terrestrial and marine vertebrates, including man, and in several invertebrate groups, particularly molluscs, crustaceans, and insects.[168] Retinol$_2$, or dehydroretinol, is found only in amphibia and freshwater fish and turtles.[169, 170] Fish which migrate from fresh to salt water, or vice-versa, during their life cycle, and amphibians which metamorphose from freshwater tadpoles to semiterrestrial adults, undergo transitions from one form of the vitamin to the other.[169, 171]

In mammals, the conversion of β-carotene to retinol occurs mainly in the mucosa of the small intestine.[172–174] The mechanism of this conversion, whether by terminal or central cleavage of the conjugated chain, is not yet settled,[175–177] although experiments with labeled β-carotene favor the central cleavage hypothesis.[178, 179, 242] Retinol is probably absorbed from the intestinal lumen in the free form, then re-esterified in the intestinal mucosa.[180, 181] In mammals, retinol appears to be preferentially esterified with palmitic acid,[181–183] although this specificity is not so pronounced in marine fish.[184] Retinol is enzymatically oxidized to the corresponding aldehyde, retinal,[185, 186] and carboxylic acid, retinoic acid.[187,–189] Recently, these relations have been thoroughly reviewed. [177]

Retinol and retinal undergo isomerization in the liver[190, 191] and in the retina,[192] where 11-cis retinal is bound to the protein opsin to form photosensitive visual pigments.[193] Retinoic acid will not function in the visual cycle, but does stimulate normal growth in vitamin A-deficient rats.[194] Retinoic acid appears to be involved in the activation of sulfate in sulfurylation reactions[195, 196] required for mucopolysaccharide synthesis.

Retinoic acid is excreted in rat bile as the retinoyl-β-glucuronide.[197] The possible metabolic functions of vitamin A are discussed in a recent review.[269]

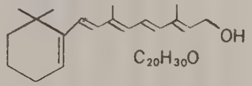
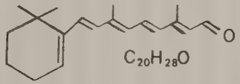
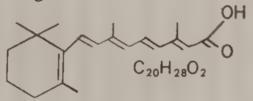
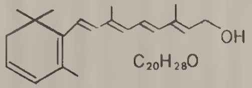
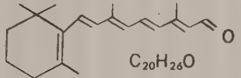
Problems encountered in the isolation of vitamin A are similar to those for carotenoids. Various methods for extraction and saponification of vitamin A from animal tissues have recently been compared,[243] and losses of the vitamin are best avoided by acetone extraction in the presence of anhydrous Na_2SO_4, followed by a brief saponification in the presence of an antioxidant.[244] Vitamin A is frequently assayed directly in the non-saponifiable mixture, but purification is necessary to eliminate carotenoids if a biological assay is used, or to eliminate spectral interference if either a spectrophotometric or colorimetric method is used. Purification is usually by chromatography, including thin-layer chromatography[265, 266] and paper chromatography.[267, 268] Losses on column chromatography can be reduced by the addition of soy bean oil.[246] Recently gas-liquid chromatography has been used for separation of retinol derivatives.[253]

Estimation of vitamin A by bioassay and spectrophotometric and colorimetric procedures is thoroughly discussed by Embree *et al.*[247] and by Moore.[248] Other colorimetric procedures have been devised[249, 250] and 9-cis isomers of vitamin A have been estimated by reaction with opsin.[251] Spectrophotometric corrections are further discussed by Wilkie.[252]

Vitamin D. Compounds of the vitamin D group are formed by the action of ultraviolet light on 3-hydroxy,Δ5,7-dienoic sterols. In man, sunlight promotes the formation of vitamin D from 7-dehydrocholesterol in the outer layers of the skin. The same reaction occurs in the fur and feathers of mammals and birds, which then obtain the vitamin orally, by grooming and preening, or by direct absorption. Several pro-vitamins D, including ergosterol and 22-dihydro-ergosterol, are found only in plants. The active vitamins can be produced artificially by ultraviolet irradiation of these sterols. Vitamins D of unknown origin and structure occur in fish liver oils. These are likely produced enzymatically instead of by irradiation.[200] 7-Dehydrocholesterol is produced from cholesterol in the animal intestine,[201, 202] while ergosterol is synthesized by yeast and other plants from squalene with lanosterol as an intermediate.[203–205] The overall biosynthesis of the vitamins D is discussed by Goodwin.[206]

Vitamin D causes an increased calcium and phosphorous absorption from the intestine,[207, 208] and also affects phosphatase reactions.[209] In addition, vitamin D promotes phosphate reabsorption from the kidney tubules. The relationships of these reactions with normal bone formation are not yet firmly established. The actions of vitamin D and parathyroid hormone on calcium and phosphate metabolism have been discussed by Albright and Reifenstein.[210]

Table II. Properties of Some Vitamin A-Active Compounds

Name	Synonyms	Formula	Mol. wt.	Crystallization	m.p.	Absorption maximum [30] $m\mu$	$E^{1\%}_{1\ cm}$	Carr-Price absorption maximum [30] $m\mu$	$E^{1\%}_{1\ cm}$	Vitamin A activity relative to retinol$_1$
Retinol$_1$	Vitamin A Axerophthol	 $C_{20}H_{30}O$	286.44	needles from MeOH	63–64	EtOH 325 EtOH 324–5	1830 1800 [254]	618	4400	100%
						retinyl acetate:		620	4420 [254]	87.4% [258]
Retinal$_1$	Vitamin A_1 aldehyde retinene$_1$ axerophthal	 $C_{20}H_{28}O$	284.42	orange-red needles from light petrol	61–62 [257]	EtOH 385 C_6H_{12} 373 $CHCl_3$ 389	1400 1548 1303	664	3400	84%
Retinoic acid	Vitamin A_1 acid	 $C_{20}H_{28}O_2$	300.42	bright yellow needles from MeOH [255]	179–180 [198] 181–182 [255]	EtOH 353 EtOH 351 C_6H_{12} 357 [255]	1510 1540 [198]	—	—	42.8% (oral) [198] 123% (intraperitoneal)
Retinol$_2$	Vitamin A_2	 $C_{20}H_{28}O$	284.42	—	—	EtOH 287 351 $CHCl_3$ 406	820 1460	693	4100	39% [259]
Retinal$_2$	Vitamin A_2 aldehyde retinene$_2$	 $C_{20}H_{26}O$	282.41	orange-red prisms from pentane [256]	77–78 [256]	C_6H_{12} 386 $CHCl_3$ 405	1440	735–705	3270	see [260]
Kitol	dimer of vitamin A_1? occurs in mammalian liver oils	$C_{40}H_{60}O_2$ [334]	572.88	elongated prisms	88–90	EtOH 290	—	—	—	—

The vitamins D and their precursors are not readily isolated from natural sources because of their low concentrations. The procedure may involve saponification, partition, digitonide precipitation, and preparation and purification of a 3,5-dinitrobenzoate derivative which is then hydrolyzed before crystallization of the vitamin.[261–264] Instead, vitamins D are usually synthesized from cholesterol or other readily obtained sterols.

The determination of vitamin D is most frequently by bioassay, although in high concentrations, it can be assayed by spectrophotometric and colorimetric means.[270] Vitamins D_2 and D_3 can be separated and determined by gas-liquid chromatography.[332] Provitamins D are assayed by colorimetry, spectrophotometry, or digitonide precipitation.[271] These various methods have been compared and discussed by reviewers.[272, 273] Conditions for extraction and saponification of vitamin D with minimal degradation are described by Chen *et al.*[274]

Vitamin E, Tocopherol. Tocopherols are widely distributed in plant tissues with small amounts occurring in animal tissues such as muscle and blood. It was established in the early 1920's that this lipid-soluble factor was required for normal reproduction in rats,[211, 212] and since then eight naturally-occurring tocopherols have been demonstrated in cereal grains.[213–215] Very little is known about the biosynthesis and metabolism of tocopherols. The variety of tocopherols found in barley, wheat, and pea seeds and seedlings diminishes as the plants grow,[216] while the contents of α-tocopherol and total tocopherol increase.[216–218] Tocopherol metabolites of unknown structure have been noted in animals.[220, 221] In mammals, tocopherol is transported by the serum lipoproteins.[219]

In vitamin E deficiency, sterility and muscular dystrophy result. A number of other effects may also be related to deficiency of the vitamin.[222] The mechanism for vitamin E activity most probably involves the antioxidant capacity of the tocopherols. α-Tocopherol protects various lipids, including vitamin A, from oxidation in air.[223–225] In addition, tocopherols may activate muscle cytochrome C reductase.[226, 227]

The tocopherols from the unsaponifiable portions of natural oils can be purified by chromatography,[283] fractional crystallization,[284] or molecular distillation.[285] Tocopherol can be separated from other fat-soluble vitamins and identified by paper chromatography.[294] Because they exhibit very low melting points, the tocopherols are usually crystallized as allophanate or phenylazobenzoate derivatives, although α- and γ-tocopherols have been obtained in crystalline form.[284, 286]

The most commonly used method of estimation of tocopherols is based on the reduction of ferric to ferrous ions in the presence of α, α-dipyridyl.[287, 288] The red color produced is measured spectrophotometrically. Ferricyanide[289] and phosphomolybdic acid[290] have also been used for color reactions with tocopherol. A thorough review of the colorimetric methods and of bioassay is presented by Gyorgy.[273]

Table III. Properties of Some Vitamins D and Precursors

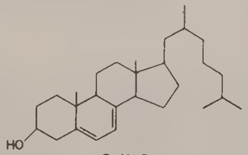
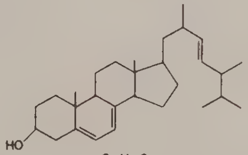
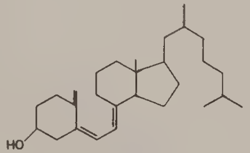
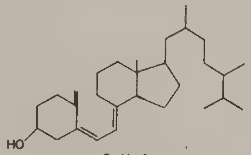
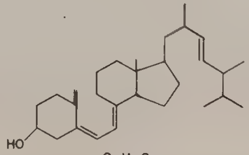
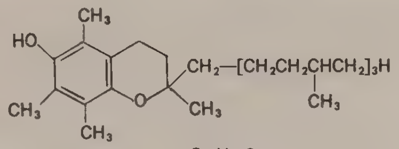
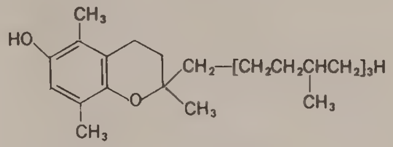
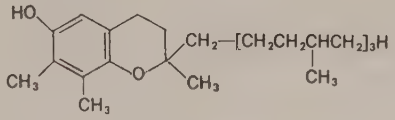
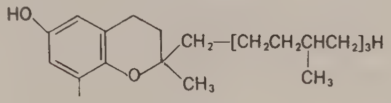
Name	Synonyms	Formula	Mol. wt.	Crystallization	m.p.	Absorption Maxima	$[\alpha]_D^t$
7-dehydrocholesterol	provitamin D_3	 $C_{27}H_{44}O$	384.62 402.64 (hydrate)	platelets from ether-MeOH	149–150 [279]	EtOH 262.5 271 281.5 293 [280]	-124^{20} ($CHCl_3$) [279]
Ergosterol	provitamin D_2 ergosterin	 $C_{28}H_{44}O$	396.63 414.65 (hydrate)	white needles from ether, $CHCl_3$ or acetone	165 [277]	EtOH 262 271 282 293.5	-135^{20} ($CHCl_3$) -174^{20} ($CHCl_3$) [278]
Vitamin D_3	cholecalciferol	 $C_{27}H_{44}O$	384.62	needles from MeOH	84–85 [281]	EtOH 265 [278]	$+84.8^{20}$ (acetone) [281]
Vitamin D_4	irradiated 22-dihydro-ergosterol	 $C_{28}H_{46}O$	398.65	long needles from acetone	96–98 [282]	EtOH 265	$+85.7^{21}$ (acetone)
Vitamin D_2	calciferol	 $C_{28}H_{44}O$	396.63	colorless needles from MeOH	121 [275]	EtOH 265, $E_{1\,cm}^{1\%} = 490$ [275]	$+106^{20}$ (EtOH) [276] $+125^{20}$ (EtOH) 5461

Table IV. Properties of Tocopherols

Name	Synonyms	Formula	Mol. wt.	m.p.	Absorption maxima* mμ [286]	$[\alpha]^{25}_{5461}$ [286]
α-tocopherol	5,7,8-trimethyltocol**	 $C_{20}H_{50}O_2$	430.69	2.5–3.5 [284] Allophanate 157–8	EtOH 292	+0.32 (EtOH) −3.0 (benz)
β-tocopherol	5,8-dimethyltocol	 $C_{28}H_{48}O_2$	416.66	Allophanate 138–9	EtOH 297	+2.9 (EtOH)
γ-tocopherol	7,8-dimethyltocol	 $C_{28}H_{48}O_2$	416.66	−3 to −2 [284] Allophanate 136–7	EtOH 298	+2.2 (EtOH) −2.4 (benz)
δ-tocopherol	8-methyltocol	 $C_{27}H_{46}O_2$	402.64	phenylazobenzoate 41–42 [291]	EtOH 298 [291]	+3.4 (EtOH) [291] +1.1 (benz)

*IR spectra have also been obtained [292, 293].

**Tocol is an accepted name for 2-methyl-2-(4′,8′,12′-trimethyldecyl)-6-chromanol.

Vitamin K. Vitamin K, or antihemorrhagic factor, occurs naturally in both plant and animal sources.[228–231] Vitamin K_1 occurs throughout the leaves of alfalfa, including the chloroplasts,[232] and also occurs with other vitamins K in many bacteria.[233,295] Egger[335] has studied the distribution of vitamins K in various plants. Two different vitamins K, designated $K_{2(35)}$ and $K_{2(30)}$, occur in putrefied fish meal.[234, 235] The more abundant form has a 35-carbon side chain, whereas a second form occurring only in small amounts has a 30-carbon side chain. The characteristics of the K-vitamins are discussed by Isler and Wiss.[236]

Vitamin K is synthesized by green leaves in the light.[237] Animals degrade administered vitamins K to menadione (vitamin K_3), then resynthesize an unsaturated side chain (of the K_2 type) of 20 carbon atoms.[238, 239] Vitamin K may act as an electron carrier in biological oxidations,[240, 241] and also is involved in the activation of proconvertin (factor VII) in the production of prothrombin.[238] The metabolic relationships of the various K vitamins have been recently discussed.[299]

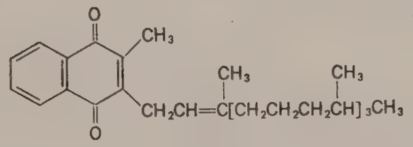
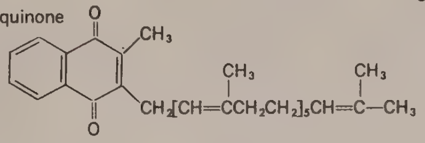
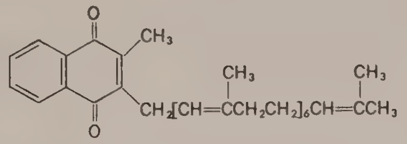
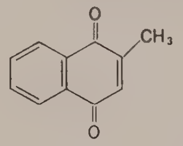
The K vitamins are isolated by chromatography of an unsaponified ether extract of a dried biological sample. Various adsorbents have been used,[296] although some, like Decalso and alumina,[297] promote decomposition of the vitamin during chromatography. The different forms of vitamin K can be separated from each other by reversed phase partition chromatography on paper impregnated with silicone.[295, 298]

Vitamin K is most frequently estimated by bioassay using young chicks. In most other animals, synthesis of the vitamin by intestinal microorganisms is sufficient to supply the requirements for this vitamin. Bioassay of the vitamin is thoroughly discussed by Gyorgy[273] and by Almquist.[300] Vitamin K can be estimated from its ultraviolet spectrum,[236, 295] although the absorption decreases rapidly upon exposure to ultraviolet light.[300] The vitamins K exhibit absorption maxima at 243, 248, 260, 269 and 325 mμ; the 248 mμ peak is frequently used for estimation. Colorimetric assays of the vitamins K have used reactions with sodium ethylate,[301] sodium diethyl dithiocarbamate,[302] and xanthene hydride.[319] The synthetic vitamin K_3, menadione, can be estimated colorimetrically using 2,4-dinitrophenylhydrazine.[303]

III. PROSTAGLANDINS

The term prostaglandin was first applied in 1935 to a lipid-soluble acidic fraction of human seminal plasma which stimulated smooth muscle contraction and caused blood pressure to fall.[304–306] Six different structurally related prostaglandins (PGE_1, PGE_2, PGE_3, $PGF_{1\alpha}$, $PGF_{2\alpha}$, $PGF_{3\alpha}$) were isolated in pure form between 1957 and 1964 from vesicular glands or lung tissue.[307–309] Although present in highest concentrations in vesicular

Table V. Properties of the Vitamins K

Name	Synonyms	Formula	Mol. wt.	Crystallization	m.p.	$E_{1\,cm}^{1\%}$, 248 mμ[a]	$[\alpha]_D$
Vitamin K_1	2-methyl-3-phytyl-1,4-naphthoquinone phylloquinone	 $C_{31}H_{46}O_2$	450.71	yellow oil	−20	420	-0.71^{21} [236]
Vitamin $K_{2(30)}$	2-methyl-3-farnesylfarnesyl-1,4-naphthoquinone	 $C_{41}H_{56}O_2$	580.90	yellow crystals from EtOH	50 [235]	319 [235]	—
Vitamin $K_{2(35)}$	2-methyl-3-farnesylgeranylgeranyl-1,4-naphthoquinone	 $C_{46}H_{64}O_2$	649.02	yellow crystals from pet. eth.	54 [235]	295 [235]	—
Vitamin K_3	2-methyl-1,4-naphthoquinone menadione	 $C_{11}H_8O_2$	172.19	yellow crystals	106	1100	—

[a] The molar extinction coefficient for the 1,4-naphthoquinone system at 248 mμ is about 1900 [236].

Table VI. Structural Relationships of Prostaglandins

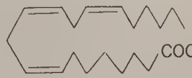
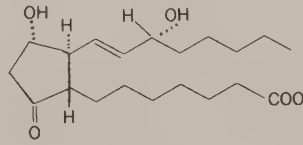
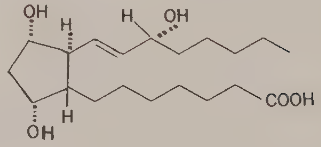
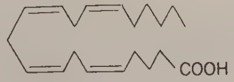
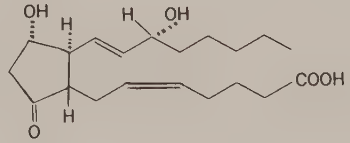
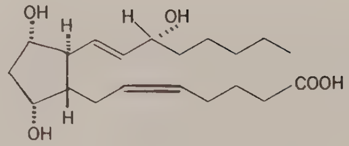
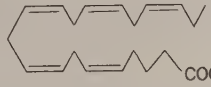
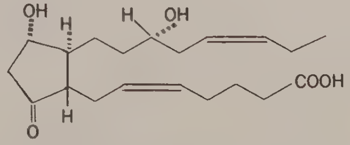
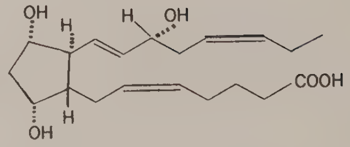
Fatty acid precursor	PGE series	PGF series
 8,11,14-eicosa-trienoid acid (homo-γ-linolenic)	 PGE_1	 $PGF_{1\alpha}$
 5,8,11,14-eicosa-tetraenoic acid (arachidonic)	 PGE_2	 $PGF_{2\alpha}$
 5,8,11,14,17-eicosa-pentaenoic acid	 PGE_3	 $PGF_{3\alpha}$

Table VII. Physiological Properties of the Prostaglandins

Prostaglandin tested	Tissue or Organism	Effect	Reference
PGE_1	man	tachycardia; reddening of face; headache; fall of arterial blood pressure and cardiac output	320, 323
PGE_1	cat	reduces duration of contraction of nictitating membrane after sympathetic nervous stimulation	326
PGE_1, PGE_2, PGE_3	rabbit guinea pig	stimulates contraction of jejunum and ileum; reduces blood pressure and heart rate	321
PGE_1	toad bladder	diminishes the increase in permeability to water induced by vasopressin and theophylline	331
PGE_1	rat epididymal fat pad	reduces basal fat mobilization; inhibits stimulation of same by epinephrine, norepinephrine, ACTH, glucagon, and TSH	322
PGE series PGF series	dog	blocks norepinephrine-stimulated increase of plasma FFA concentration (PGF series only 1/10 as active)	324, 325

glands and seminal plasma, the prostaglandins are widely distributed in mammalian organs.[310] The relationship between prostaglandins and the essential fatty acids was established by the demonstrated conversions of homo-γ-linolenic, arachidonic, and eicosa-8,11,14-trienoic acids into prostaglandins (PGE_1, PGE_2 and PGE_3, respectively).[311, 312] The structural relationships of various prostaglandins and fatty acids are shown in Table VI. After subcutaneous or intravenous administration of tritium-labeled PGE_1 to rats, labeled products occur in kidney, liver, lungs, pituitary, adrenals, ovaries, uterus, heart and other organs. Labeled metabolites were found mainly in the urine, with some excretion also via the bile.[313] Conversion of PGE_1 into two metabolites by a soluble enzymatic system of guinea pig lung has been demonstrated.[314] The chemistry and physiology of the prostaglandins have been recently reviewed.[315]

For the isolation[309] of prostaglandins, a tissue homogenate is suspended in ethanol and stirred. The supernatant is then concentrated and extracted once with ethyl acetate to remove neutral lipids. The solution is then acidified (pH 3) and re-extracted with ethyl acetate. The extract is washed with buffer (pH 8) and the buffer is then acidified and extracted with ethyl acetate. After partition of this extract between petroleum ether and 66% ethanol, the aqueous phase is acidified and extracted with ether. The ether extract, washed with water until neutral, contains prostaglandin, which is then purified chromatographically.[316]

The prostaglandins have been separated and characterized by thin-layer chromatography on silver nitrate-impregnated silica gel.[317] Quantitative spectrophotometric estimation of PGE_1, PGE_2, and PGE_3 is possible after alkali isomerization.[318] Gas-liquid chromatography of trimethylsilyl ether derivatives of $PGF_{1\alpha}$, $PGF_{2\alpha}$, and $PGF_{3\alpha}$ methyl esters also permits quantitative estimation.[309, 318] The biological activity of the prostaglandins is determined by the relative stimulation of isolated duodenal strips from rabbits compared to a standard preparation of prostaglandin.[307] The physiological properties, recently reviewed by Bergstrom and Samuelsson,[315] are briefly summarized in Table VII.

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46. TRACE ANALYSIS OF COPPER, MANGANESE, AND ZINC IN OYSTER SHELLS BY ATOMIC ABSORPTION SPECTROPHOTOMETRY. Douglas A. Wolfe, Twyla A. Miner, Bureau of Commercial Fisheries, Radiobiological Laboratory, Beaufort, North Carolina 28516.

In atomic absorption analyses for trace levels of Cu, Mn, and Zn in nitric acid digests of oyster shells, instrumental response was non-linear with concentration. Since oyster shells are about 98% $CaCO_3$, standard solutions of Cu, Mn, and Zn containing various amounts of $Ca(NO_3)_2$ were analyzed. Two antagonistic phenomena contributed to the non-linear response. 1. Aspiration rate decreased proportionally with increasing density and viscosity of solution and thereby decreased the number of absorbing atoms in the flame. 2. The high concentrations of $Ca(NO_3)_2$ scattered the light emitted by the hollow cathode and generated a spurious absorption. The magnitude of this non-specific scattering was nearly proportional to the fourth power of the wavelength; therefore, analyses of the three elements were affected differentially.

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NUTRIENT ELEMENTS IN SEAWATER

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191. NUTRIENT ELEMENTS IN SEAWATER

Data are for those elements that may be essential to the nutrition of marine life, including some (aluminum, fluorine, nickel, selenium, strontium, and vanadium) for which physiological functions are poorly understood. **Probable Chemical State** is based largely on the calculations of Sillen for a hypothetical oceanic model at equilibrium [41, 122]. Nitrogen and phosphorus fluctuate independently of salinity because these elements are constantly cycled by living organisms, and, during peak biological activity, their concentration in seawater may be drastically depleted. **Source of Sample**: N = north(ern); E = east(ern); S = south(ern); W = west(ern). **Chlorinity Ratio**: The major elements usually occur in constant proportions and are reported in terms of a chlorinity ratio, where chlorinity is the total halide content expressed as chloride. **Concentration**: Trace elements are reported as mg/L, unless otherwise specified. **Analytical Method**: EDTA = ethylenediaminetetraacetic acid. Values in parentheses are ranges, estimate "b" or "c" as indicated (*see* Introduction). For additional information on the composition of seawater, consult references 41, 51, 54, 55, 90, 104, 108, 137; on laboratory procedures, references 101, 131.

	Element [Probable Chemical State]	**Source of Sample**	**Chlorinity Ratio** g/unit Cl [**Concentration**, mg/L]	**Analytical Method**	**Reference**
1	Aluminum	Akashi City, Japan, offshore	[(0.295-0.325)^c]	Aluminon lake colorimetry	58, 59
2		Sea of Japan	[(0.315-0.360)^c]		
3		Atlantic Ocean, coast of USA, surface	[(0-0.010)^c]	Pontachrome blue-black R fluorometry	123
4		Indian Ocean, surface	[0.0268]	8-Quinolinol colorimetry	67

continued

191. NUTRIENT ELEMENTS IN SEAWATER

	Element [Probable Chemical State]	Source of Sample	Chlorinity Ratio g/unit Cl [Concentration, mg/L]	Analytical Method	Reference
5	Aluminum	Pacific Ocean, NE; San Juan Channel, Washington; 0-2000 meters	[0.540(0.162-1.512)^{c}]	Oxine precipitation diazotized; sulfanilic acid colorimetry	47
		Pacific Ocean, off California		Pontachrome blue-black R fluorometry; millipore filtration	117
6		Inshore: particulate	[>0.100]		
7		Offshore: particulate	[0.002]		
8		Inshore: soluble	[0.0025]		
9		Offshore: soluble	[0.0005]		
10		Pacific Ocean, off California	[(0.0002-0.0043)^{c}]	Pontachrome blue-black R fluorometry; millipore filtration	118
11		Pacific Ocean, off California, & Weddell Sea, Antarctic: soluble	[0.001(0-0.003)^{b}]		
12		Weddell Sea, Antarctic: particulate	[(0.0040-0.120)^{c}]		
13		Puget Sound, Washington: soluble	[0.006(0.002-0.010)^{f}]		
14		San Juan Archipelago, Washington	[1.90]	Aluminum method of Yoe & Hill	142
15		Sea of Japan	[(0.005-0.0252)^{c}]	8-Quinolinol colorimetry	52
16	Boron [H_3BO_3; $H_2BO_3^-$]	Arctic Ocean: H_3BO_3	0.00148	Mannitol titration	45
17		Norway, coastal waters: H_3BO_3	0.00141	....	
18		Arctic Ocean, surface: total B (as H_3BO_3)	0.001425	....	40
		Gulf of Alaska, surface			
19		Inorganic B (as H_3BO_3)	(0.001348-0.001367)^{c}	....	
20		Total B (as H_3BO_3)	(0.00138-0.00140)^{c}	....	
21		Pacific Ocean, off Hawaii, surface: inorganic B (as H_3BO_3)	(0.00136-0.00137)^{c}	....	
22		Pacific Ocean, Hawaii to California, surface: total B (as H_3BO_3)	0.001374	....	
23		Gulf of Mexico	[(4.643-4.683)^{c}]	....	94
24		Pacific Ocean, W: H_3BO_3	0.00136	....	86
25		Indian Ocean	[2.2]	Titration in presence of mannitol	67
26		Indian Ocean, W; 16°58′S, 64°42′E, 3958 meters: H_3BO_3	0.00135 (0.00134-0.00136)^{b}	Boron-oxalate-curcumin complex formed in molten phenol, 120°C; spectrophotometric in ethyl alcohol solution	44
27	Bromine [Br^-]	Bering Sea; Bering Straits; Puget Sound, Washington; Pacific Ocean, NE: Br^-	0.00340	Hypochlorite-iodide oxidimetry; iodine titrated with thiosulfate	140
28		Great Britain, coastal waters: Br^-	0.00343	Hypochlorite-iodide oxidimetry; thiosulfate titration	53
29		Indian Ocean	[43.6]	Iodometric determination of bromate	67
30		Japan, coastal waters; Tokyo Bay: Br^-	0.00347 (0.00340-0.00354)^{b}	....	80
31	Calcium [Ca^{++}; $CaSO_4$]	Antarctic Ocean	[10.3(10.2-10.4)^{c} [1]]	Flame photometry [132]	136
32		Indian Ocean	[10.2(10.1-10.4)^{c} [1]]		
33		Pacific Ocean	[10.1(9.7-10.8)^{c} [1]]		
34		Atlantic Ocean, 48°12′N, 127°17′W: Ca^{++}	0.02134 (0.02109-0.02159)^{b}	Complexometric titration with (ethylenedinitrilo)tetraacetate to blue end point of Cal-red indicator	98
35		Atlantic Ocean, off the Bahamas: Ca^{++}	0.02122	Ion exchange chromatography; EDTA titration with Na purpurate	17
36		Chesapeake Bay, Maryland & Virginia: Ca^{++}	0.02119		
37		Gulf of Alaska: Ca^{++}	0.02188 (0.02172-0.02204)^{b}	Flame photometry	24
38		Tokyo Bay, Japan: Ca^{++}	0.02136	....	78
39		Vigo Estuary, Spain: Ca^{++}	0.02000	Complexometric titration with EDTA; calcein indicator	103
40	Carbon [HCO_3^-; H_2CO_3; CO_3^{--}; CO_2 gas; organic C compounds]	Atlantic Ocean, off Bermuda	[2.35(2.21-2.49)^{b} [2]]	Ceric-chromic-sulfuric acid combustion; titration of $BaCO_3$ with HCl [72]	71
41		Atlantic Ocean, surface	[1.5 [2,3]]	Dry combustion method	128
42		Black Sea, 0-200 meters	[3.5 [2,3]]		
43		Black Sea	[(2.83-3.36)^{c} [2]]	....	29
44		Atlantic Ocean	[(2.40-2.48)^{c} [2]]	Dry combustion method	125
45		Greenland Sea	[(2.0-2.1)^{c} [2]]		
46		Pacific Ocean	[(0.98-2.68)^{c} [2]]		

[1] mg-atoms/kg. [2] Dissolved organic carbon (or C). [3] Decreases with depth.

continued

191. NUTRIENT ELEMENTS IN SEAWATER

	Element [Probable Chemical State]	Source of Sample	Chlorinity Ratio g/unit Cl [Concentration, mg/L]	Analytical Method	Reference
47	Carbon [HCO$_3^-$; H$_2$CO$_3$; CO$_3^{--}$; CO$_2$ gas; organic C compounds]	Atlantic Ocean, N	[1.56(0.99-2.71)[c] [2]]	Dry combustion method	127
48		Baltic Sea	[4.35(3.52-6.63)[c] [2]]		
49		North Sea	[3.40(2.40-4.16)[c] [2]]		
50		Atlantic Ocean, N	[(0.20-1.30)[c] [2]]	Coulometric titration of CO$_2$ after chromic-sulfuric acid digestion	35
51		North Holland Canal	[24.0[2]]		
52		North Sea	[(0.50-1.80)[c] [2]]		
53		Norwegian Sea	[(0.45-1.38)[c] [2]]		
54		Wadden Sea, Netherlands	[(1.0-8.0)[c] [2]]		
55		Aransas Pass, Texas	[1.4(1.3-1.5)[c] [2]]	Infrared absorption of CO$_2$; wet combustion	151
		Baffin Bay, Texas			
56		Filtered	[(26.3-38.7)[c] [2]]		
57		Unfiltered	[(80.0-91.5)[c] [2]]		
58		Laguna Madre, Texas	[14.9(13.2-17.3)[c] [2]]		
59		Redfish Bay, Texas	[6.3(6.1-6.5)[c] [2]]		
60		Pacific Ocean, 3 stations	[(0.6-2.7)[c] [2]]	*See* reference 72	100
61		Tokyo Bay: HCO$_3^-$	0.00741[4]	....	78
62	Cobalt [Co^{++}; CoSO$_4$]	Barents Sea	[0.0015]	....	77
63		Black Sea	[0.0035]	....	
64		Black Sea	[(0.0016-0.0040)[c]]	Toluene extraction; β-nitroso-α-naphthol colorimetry	116
65		Sea of Azov, USSR	[(0.0024-0.0045)[c]]		
66		Gullmarfjord, Sweden, shallow water	[0.0001]	Optical & X-ray spectrography; chemical separation	93
67		Pacific Ocean	[(0.00038-0.00067)[c]]	Fe(OH)$_3$ coprecipitation; dithizone-CHCl$_3$ extraction; thiocyanate-stannous chloride colorimetry	57
68		Pacific Ocean, off California	[0.000038]	Ion exchange; nitroso-R-salt colorimetry [121]	150
69		Plymouth, England, offshore	[<0.0003]	Spectrography	12
70		Puget Sound, San Juan Archipelago, Washington	[0.00028 (0.00024-0.00032)[c]]	Dithizone extraction; nitroso-R-salt colorimetry	141
71	Copper [Cu^{++}; CuSO$_4$]	Adriatic Sea, central	[0.0056(0-0.0077)[c]]	Ethyl acetate extraction; diethyldithiocarbamate colorimetry	81
72		Antarctic Ocean	[(0.0011-0.0012)[c]]	Fe(OH)$_3$ coprecipitation & activation	55
73		Atlantic Ocean	[(0.0005-0.0016)[c]]		
74		Gulf of Mexico	[(0.0004-0.0011)[c]]		
75		Atlantic Ocean	[0.0036]	Spectrography	152
76		Atlantic Ocean	[0.00167 (0.0011-0.0021)[c]]	Atomic absorption	37
77		Atlantic Ocean, off the Bahamas	[(0.001-0.008)[c]]	Electrolytic concentration; diethyldithiocarbamate colorimetry	39
78		New England coast	[(0.008-0.034)[c]]		
79		Baltic Sea	[(0.0015-0.0078)[c]]	Dithizone colorimetry	16
80		Baltic & North Seas	[(0.006-0.026)[c]]	Spectrophotometry	84
81		English Channel	[(0-0.036)[c]]	Amyl alcohol extraction; sodium-diethyldithiocarbamate colorimetry	5
82		English Channel, seasonal variation	[(0.0015-0.0248)[c]]	*See* reference 5	6
		English Channel, off Plymouth		2,2′-Diquinolyl colorimetry	76
83		Particulate	[0.0003]		
84		Total	[0.0012]		
85		Friday Harbor, Seattle, Washington	[(0.00076-0.0019)[c]]	Xylene extraction; diethyldithiocarbamate colorimetry	21
86		Gulf of Mexico, N	[(0.001-0.0156)[c]]	*See* reference 5	106
87		Gulf of Mexico, ultrafiltrable, nondialyzable	[0.015]	....	55
88		Gullmarfjord, Sweden, shallow water	[0.004]	Optical & X-ray spectrography; chemical separation	93
89		Indian Ocean	[0.030]	*See* reference 21	67
90		Kuroshio current, Pacific Ocean, W, vertical variation	[(0.0005-0.0007)[c]]	Dithizone colorimetry	89
91		Sagami & Suruga Bays, Japan	[(0.0003-0.0015)[c]]		
92		Kuroshio current, Pacific Ocean, W	[(Trace-0.030)[c]]	....	85, 86
93		Atlantic Ocean, N	[(0.010-0.030)[c]]	*See* reference 84	65
94		Sargasso Sea, Atlantic Ocean, N	[(<0.003-0.012)[c]]		

[2] Dissolved organic carbon (or C). [4] Dissolved CO$_2$ content varies with pH and temperature, but also exhibits a constant chlorinity ratio.

continued

191. NUTRIENT ELEMENTS IN SEAWATER

	Element [Probable Chemical State]	Source of Sample	Chlorinity Ratio g/unit Cl [Concentration, mg/L]	Analytical Method	Reference
95	Copper [Cu^{++}; $CuSO_4$]	San Juan Channel, Washington, seasonal variation	[(0.0010-0.0018)[c]]	*See* reference 21	22
96		Scotland, coastal waters	[0.0064]	H_2SO_4 digestion; diethyldithiocarbamate colorimetry	9
97		Tokyo Bay, Japan	[0.0024(0.001-0.0057)[c]]	....	88
98	Fluorine [F^-]	British Columbia & Washington, coastal & inland water: F^-	0.00007 [1.4]	Bleaching by fluoride of zirconium-alizarin lake, colorimetrically	143
99		Pacific Ocean, off British Columbia	[(1.416-1.547)[c]]		
100		Clear seawater	[1.58]	Spectrophotometric determination by bleaching of zirconium-alizarin lake [1]	13
101		At great depths	[1.47]		
102		Indian Ocean	[0.800]	*See* reference 1	67
103		Tokyo Bay, Japan	[(0.789-1.36)[c]]	*See* reference 1	79
104	Iodine [I^-; IO_3^-]	Adriatic Sea, Croatian coast	[0.061]	Colorimetric determination of excess Ce^{++++} after reaction with I^-	34
105		Antarctic Ocean, south of 52°S latitude: total I	[0.43(0.40-0.45)[c][5]]	*See* reference 133	136
		Indian Ocean: total I			
106		North of 42°S latitude	[0.40(0.34-0.44)[c][5]]		
107		South of 42°S latitude	[0.43(0.40-0.45)[c][5]]		
		Pacific Ocean, NW: total I			
108		North of 20°N latitude	[0.31(0.21-0.37)[c][5]]		
109		South of 20°N latitude	[0.22(0.06-0.34)[c][5]]		
110		Antarctic Ocean, south of 52°S latitude: I^-	[0.10(0.06-0.14)[c][5]]	*See* reference 133	136
		Indian Ocean: I^-			
111		North of 42°S latitude	[0.16(0.13-0.19)[c][5]]		
112		South of 42°S latitude	[0.11(0.08-0.12)[c][5]]		
		Pacific Ocean, NW: I^-			
113		North of 20°N latitude	[0.10(0.02-0.25)[c][5]]		
114		South of 20°N latitude	[0.09(0.04-0.17)[c][5]]		
115		Atlantic Ocean	[0.043]	Winkler method: IO_3^- reduced with arsenious acid & HCl; iodide oxidized to iodine with HNO_3; extracted with CCl_4; determined colorimetrically	102
		Arctic Ocean: IO_3^-		Amperometric titration	7,8
116		5 meters	[0]		
117		100 meters	[0.0252]		
118		500 meters	[0.0642]		
119		1500-2000 meters	[0.0465]		
120		Pacific Ocean, N; inland Washington: IO_3^-	[0.035(0.020-0.043)[c]]		
		Arctic Ocean: Pacific Ocean, N: total I		Br_2 oxidation of I^- to IO_3^-; amperometric titration of IO_3^-	7,8
121		Surface	[0.059(0.051-0.076)[c]]		
122		10-150 meters	[0.058(0.051-0.068)[c]]		
123		200-4000 meters	[0.063(0.058-0.068)[c]]		
124		Washington, inland, 0-45 meters	[0.045(0.039-0.066)[c]]		
125		Barents Sea	[0.063]	....	146
126		India, coastal waters	[(0.045-0.053)[c]]	*See* reference 7	66
127		Indian Ocean	[0.044]	Colorimetric determination of excess Ce^{++++} after reaction with I^-	67
128		White Sea, USSR, surface	[(0.025-0.026)[c]]	....	124
		3°38′N, 141°56′E, surface		Precipitation of I^- with $AgNO_3$-AgCl; oxidation to IO_3^- with Br; I liberated by CdI_2; determined spectrophotometrically [133]	135
129		I^-	[0.0076]		
130		IO_3^-	[0]		
131	Iron [$Fe(OH)_3$] (solid state)	Atlantic Ocean, coastal USA: soluble	[0.0026(0-0.007)[c]]	*o*-Phenanthroline colorimetry	123
132		Atlantic Ocean: total Fe	[0.0062 (0.0056-0.0073)[c]]	Atomic absorption	37

[5] µg-atoms/kg.

continued

	Element [Probable Chemical State]	Source of Sample	Chlorinity Ratio g/unit Cl [Concentration, mg/L]	Analytical Method	Reference
133	Iron [$Fe(OH)_3$] (solid state)	Bay of Biscay: particulate	[(0.001-0.290)^{c}]	*o*-Phenanthroline colorimetry after $NH_2OH \cdot HCl$ reduction	3
134		English Channel: particulate	[0.050(0.019-0.158)^{c}]		
		Bering Sea: particulate		*See* reference 75	68
135		<200 meters	[0.0287]		
136		>200 meters	[0.0122]		
137		Black Sea, surface: particulate	[0.030]	2,2′-Dipyridyl colorimetry	33
138		Black Sea, 1000-2000 meters: soluble	[(0.0059-0.020)^{c}]	*o*-Phenanthroline colorimetry	33
		English Channel, W		2,2′-Dipyridyl colorimetry	27
139		0-50 meters	[0.0132(0.0016-0.0248)^{b}]		
140		60-75 meters	[0.0244(0.0064-0.0424)^{b}]		
141		Bottom layer	[0.0270(0-0.0672)^{b}]		
142		Gullmarfjord, Sweden, shallow water	[0.008]	Optical & X-ray spectrography after chemical separation	93
143		Indian Ocean	[0.160]	Thiocyanate colorimetry	67
		Pacific Ocean, N		2,2′-Dipyridyl colorimetry; membrane filtration	75
144		<500 meters: particulate	[(0-0.050)^{c}]		
145		<500 meters: soluble	[0.0033(0.0007-0.0055)^{c}]		
146		>500 meters: particulate	[0.0045]		
147		>500 meters: soluble	[0.0037]		
		Pacific Ocean, NE		Millipore filtration. *See also* reference 75.	74
148		Particulate	[0.1141]		
149		Soluble	[0.0178]		
		Pacific Ocean, Panama bight: particulate		*See* reference 75	119
150		Shallow water	[0.0195]		
151		Deep water	[0.0074]		
152		Sargasso Sea, Atlantic Ocean, N: particulate	[0.0019]	2,2′-Dipyridyl colorimetry; millipore filtration; $NH_2OH \cdot HCl$	82
153		Sargasso Sea, Atlantic Ocean, N: soluble	[0.0017]	Bathophenanthroline colorimetry; $NH_2OH \cdot HCl$ reduction	82
154	Magnesium [Mg^{++}; $MgSO_4$]	Atlantic Ocean, 49°12′N, 127°17′W: Mg^{++}	0.06689 (0.06665-0.06713)^{b}	Complexometric titration with (ethylenedinitrilo)tetraacetate & eriochrome blue-black B; subtract Ca + Sr	99
155		Pacific Ocean, NE: Mg^{++}	0.0669	....	85
156		Pacific Ocean, NW: Mg^{++}	0.0676	....	
157		Tokyo Bay, Japan: Mg^{++}	0.06697	....	78
158		Vigo Estuary, Spain: Mg^{++}	0.06719	Complexometric titration with EDTA; eriochrome black T	103
159	Manganese [Mn^{++}; $MnSO_4$]	Atlantic Ocean	[0.0036(0.003-0.0044)^{c}]	Atomic absorption	37
160		Baltic Sea	[(0.0015-0.016)^{c}]	*See* reference 144	70
		Black Sea			126
161		0-50 meters	[<0.0005]	....	
162		100-300 meters	[(0-0.0005)^{c}]	....	
163		>500 meters	[<0.0002]	....	
164		Black Sea: soluble	[(0.0005-0.0001)^{c} [3]]	....	87
165		English Channel	[(0.0007-0.0010)^{c}]	Catalysis of tetramethyldiaminodiphenylmethane oxidation	50
		Gulf of Mexico		Neutron activation analysis & $Fe(OH)_3$ coprecipitation	113
166		Surface	[(0.0008-0.0040)^{c}]		
167		3500 meters	[(0.0003-0.0014)^{c}]		
		Pacific Ocean			
168		18 meters	[0.00085]		
169		159 meters	[0.00140]		
170		2300 meters	[0.00580]		
171		4100 meters	[0.00860]		
172		5440 meters	[0.00120]		
173		Redfish Bay, Texas	[0.0062]		
174		Gullmarfjord, Sweden, shallow water	[0.003]	Optical & X-ray spectrography; chemical separation	93
175		Indian Ocean	[0.0025]	Oxidation to permanganate; determined colorimetrically	67

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[3] Decreases with depth.

continued

191. NUTRIENT ELEMENTS IN SEAWATER

	Element [Probable Chemical State]	Source of Sample	Chlorinity Ratio g/unit Cl [Concentration, mg/L]	Analytical Method	Reference
	Manganese	Pacific Ocean, N		Emission spectrography	42
176	[Mn^{++};	Surface: soluble	[0.0028]		
177	$MnSO_4$]	Surface: particulate	[0.00022]		
178		1000 meters: soluble	[0.0050]		
179		1000 meters: particulate	[0.00006]		
180		3500 meters: soluble	[0.0004]		
181		3500 meters: particulate	[0.00007]		
182		Pacific Ocean, NE	[(0.0011-0.0099)^c]	Paraperiodate oxidation; permanganate determined colorimetrically	144
183	Molybdenum [MoO_4^{--}]	Antarctic Ocean	[0.0105 (0.0096-0.0115)^c [6]]	*See* reference 134	136
184		Indian Ocean	[0.0125(0.0115-0.0125)^c [6]]		
185		Pacific Ocean, NW	[0.0096(0.0086-0.0115)^c [6]]		
186		Atlantic Ocean	[0.0039]	Spectrography	152
187		Black Sea	[0.0025]		
188		Japan, offshore	[0.0106]	$Fe(OH)_3$-hexamine coprecipitation; dithiol complex in butyl acetate colorimetry	57, 61
189		Maiko & Shirahama, Japan, offshore	[(0.010-0.011)^c]	$Fe(OH)_3$-hexamine coprecipitation; thiocyanate in butyl acetate colorimetry	57
190		Shirahama, Japan, offshore	[(0.009-0.010)^c]	$Fe(OH)_3$-hexamine coprecipitation; dithiol complex in butyl acetate colorimetry	57
191		Pacific Ocean	[0.0122 (0.0120-0.0124)^t]	α-Benzoinoxime cocrystallization; ion exchange; thiocyanate colorimetry	149
192		Plymouth, England, offshore	[(0.012-0.016)^c]	Spectrography	12
193	Nickel [Ni^{++};	Atlantic Ocean	[0.0012]	Spectrography	152
194	$NiSO_4$]	Black Sea	[0.0010]		
195		Gullmarfjord, Sweden, shallow water	[0.0005]	Optical & X-ray spectrography; chemical separation	93
		Plymouth, England		Spectrography	12
196		Inshore	[0.0015]		
197		Offshore	[(0.0050-0.0060)^c]		
198		Shirahama, Japan	[(0.0007-0.0008)^c]	$Fe(OH)_3$ coprecipitation; dimethylglyoxime & $CHCl_3$ extraction; dimethylglyoxime & C_2H_5OH colorimetry	57
	Nitrogen	Adriatic Sea: NO_3^-		*See* reference 91	38
199	[NO_3^-; NO_2^-;	0-100 meters	[0.015(0.003-0.104)^c]		
200	NH_4^+; N_2	150-950 meters	[0.031(0.010-0.063)^c]		
	gas; organic N	Ionian Sea: NO_3^-			
201	compounds]	5 meters	[0.0065(0.001-0.017)^c]		
202		75 meters	[0.0068(0.001-0.013)^c]		
203		300 meters	[0.0306(0.019-0.049)^c]		
204		Tyrrhenian Sea: NO_3^-	[0.028(0.001-0.095)^c]		
205		Tyrrhenian Sea: NO_2^-	[0.0017(0-0.0052)^c]	*See* reference 11	38
206		Atlantic Ocean, off Bermuda: organic N comp.	[0.244(0.228-0.260)^b]	Combustion at 500°C; NH_3 trapped in HBr, reacted with NaOBr; excess NaOBr titrated with acid naphthyl red [72]	71
207		Atlantic Ocean: organic N comp.	[(0.24-0.26)^c]	....	125
208		Greenland Sea: organic N comp.	[(0.03-0.38)^c]	....	
209		Pacific Ocean: organic N comp.	[(0.07-0.11)^c]	....	
210		Atlantic Ocean, N: organic N comp.	[(0.04-0.40)^c]	*See* reference 72	35
211		Norwegian Sea: organic N comp.	[(0.10-0.21)^c]		
		Black Sea: NO_2^-			32
212		Surface to 150 meters	[(0-0.002)^c]	....	
213		>150 meters	[0]	....	
214		Greenland Sea; Norwegian Sea, N: NO_2^-	[(0.001-0.002)^c]	....	56
		Indian Ocean, 34°1′S, 153°5′E: NO_3^-		Strychnidine colorimetry [49], & hydrazine colorimetry [91]	28
215		0-1300 meters	[(0-0.42)^c [7]]		
216		1300-4500 meters	[(0.35-0.448)^c]		

[6] mg/kg. [7] Increases with depth.

continued

191. NUTRIENT ELEMENTS IN SEAWATER

	Element [Probable Chemical State]	Source of Sample	Chlorinity Ratio g/unit Cl [Concentration, mg/L]	Analytical Method	Reference
	Nitrogen [NO_3^-; NO_2^-; NH_4^+; N_2 gas; organic N compounds]	Indian Ocean, N			115
217		Surface: NO_3^-	[<0.0005]	....	
218		100 meters: NO_3^-	[(0.01-0.02)^{c}]	....	
219		600 meters: NO_3^-	[(0.015-0.022)^{c}]	....	
220		50-100 meters: NO_2^-	[(0.00025-0.0005)^{c}]	....	
221		200-500 meters: NO_2^-	[(0.0001-0.00016)^{c}]	....	
222		Indian Ocean; Port Hacking, Australia, 50 meters, seasonal: NH_4^+	[(0.001-0.038)^{c}[1]]	Oxidation of NH_4^+ by hypochlorite (pH 8) to monochloramine; spectrophotometry of blue phenol; indophenol formed upon reaction of monochloramine with phenol	92
223		Pacific Ocean, off Peru: NO_3^-	[(0.336-0.700)^{c}]	Reduction of NO_3^- with Zn; NO_2^- determined spectrophotometrically with *N*-(1-naphthyl)ethylenediamine	20
224		Pacific Ocean, off Washington: organic N comp.	[(0.09-0.32)^{c}]	Kjeldahl	109
		Pacific Ocean, NE, 8-21°N latitude: NO_2^-			15
225		Surface	[0]	....	
226		30 meters, thermocline	[(0.007-0.015)^{c}]	....	
227		100 meters	[0]	....	
228		150-750 meters[2]	[(0-0.035)^{c}]	....	
229		800 meters	[0]	....	
230		Sargasso Sea, Atlantic Ocean, N: NH_4^+	[(0-0.0318)^{c}]	Pyridine-pyrazolone colorimetry [73]	83
231	Phosphorus [HPO_4^{--}; $H_2PO_4^-$; PO_4^{---}; H_3PO_4; organic P compounds]	Adriatic Sea	[0.0032(0.0009-0.015)^{c}]	*See* reference 30	38
232		Ionian Sea	[0.0026(0.0006-0.0077)^{c}]		
233		Tyrrhenian Sea	[0.0067(0.0013-0.0143)^{c}]		
234		Atlantic Ocean: organic P comp.	[(0.001-0.021)^{c}]	....	125
235		Greenland Sea: organic P comp.	[(0.0009-0.029)^{c}]	....	
236		Atlantic Ocean, N: organic P comp.	[(0-0.009)^{c}]	*See* reference 51	35
237		North Sea: organic P comp.	[(0-0.019)^{c}]		
238		Wadden Sea, Netherlands: organic P comp.	[(0.006-0.0273)^{c}]		
239		Atlantic Ocean, subtropical: organic P comp.	[(0.002-0.009)^{c}]	*See* reference 51	69
240		Indian Ocean	[0.04]	Perchloric acid digestion; phosphomolybdate colorimetry	67
241		Coral Sea, 0-10°N, 148-180°E: total P	[(0.072-0.094)^{c}]	....	110
242		Coral & Tasman Seas; 0-40°S, 148-180°E: total P	[(0.022-0.077)^{c}]	....	
		Coral & Tasman Seas: total P			111
243		300-1000 meters	[(0.013-0.082)^{c}]	....	
244		1000-5000 meters	[(0.052-0.087)^{c}]	....	
245		English Channel: organic P comp.	[(0.002-0.008)^{c}]	Digestion by autoclave: Mo blue colorimetry	51
246		Greenland Sea: Norwegian Sea, N: PO_4^{---}	[(0.005-0.020)^{c}]	....	56
		Indian Ocean			64
247		PO_4^{---}	[(0.004-0.011)^{c}]	....	
248		Total P	[(0.011-0.056)^{c}]	....	
		Indian Ocean, N			114
249		Surface: PO_4^{---}	[(0.0001-0.0004)^{c}]	....	
250		Surface: organic P comp.	[(0-0.00027)^{c}]	....	
251		Thermocline: organic P comp.	[(0.00018-0.00051)^{c}]	....	
252		200 meters: organic P comp.	[(0.00006-0.00019)^{c}]	....	
253		1000-1800 meters: PO_4^{---}	[(0.0023-0.0029)^{c}]	....	
254		Indian Ocean, SE; Pacific Ocean, SW: organic P comp.	[(0.0031-0.012)^{c}]	Perchloric acid digestion; Mo blue colorimetry	112
255		Menai Straits, Wales, inshore waters: PO_4^{---}	[(0.0031-0.020)^{c}]	Mo blue colorimetry [51]	63
		Pacific Ocean, NE, off Canada		Perchloric acid digestion; Mo blue colorimetry [48]	130
256		Surface: PO_4^{---}	[0.043(0.038-0.048)^{b}]		
257		Surface: organic P comp.	[0.031(0.022-0.040)^{b}]		

[1] Maximum in May; minimum in July. [2] Nitrite-containing layer was very low in O_2 content.

continued

	Element [Probable Chemical State]	Source of Sample	Chlorinity Ratio g/unit Cl [Concentration, mg/L]	Analytical Method	Reference
	Phosphorus [HPO_4^{--}; $H_2PO_4^{-}$; PO_4^{---}; H_3PO_4; organic P compounds]	Pacific Ocean, NE, off Canada		Perchloric acid digestion; Mo blue colorimetry [48]	130
258		20-30 meters: PO_4^{---}	[0.043(0.038-0.048)^{b}]		
259		20-30 meters: organic P comp.	[0.014(0.006-0.022)^{b}]		
260		100-150 meters: PO_4^{---}	[0.064(0.059-0.069)^{b}]		
261		100-150 meters: organic P comp.	[0.025(0.015-0.035)^{b}]		
262		900-1000 meters: PO_4^{---}	[0.096(0.089-0.103)^{b}]		
263		900-1000 meters: organic P comp.	[0.020(0.009-0.031)^{b}]		
264		1500 meters: PO_4^{---}	[0.093(0.086-0.100)^{b}]		
265		1500 meters: organic P comp.	[0.065(0.051-0.079)^{b}]		
266		2000 meters: PO_4^{---}	[0.091(0.084-0.098)^{b}]		
267		2000 meters: organic P comp.	[0.020(0.009-0.031)^{b}]		
		Plymouth, England, offshore			4
268		PO_4^{---}	[(0.004-0.014)^{c} [12]]	....	
269		Total P	[0.016 [12]]	....	
270	Potassium [K^+]	Bay of Bengal, inshore surface: K^+	0.01964	Flame photometry	46
271		Firth of Clyde, off SE shore of the Cumbrae Islands, Scotland: K^+	[0.02009 (0.01969-0.02049)^{b}]	Precipitation as potassium-silver cobaltinitrite; oxidized by Ce^{++++}; excess Ce^{++++} titrated with ferrous ammonium sulfate	148
272		Pacific Ocean, W: K^+	0.0191	....	85
273		San Juan Channel, Washington: K^+	[0.02103 (0.02057-0.02131)^{c}]	Flame photometry	19
274		Tokyo Bay, Japan: K^+	0.2021	....	78
275	Selenium [SeO_4^{--}]	Heligoland, North Sea	[(0.0033-0.0044)^{c}]	$Fe(OH)_3$ coprecipitation or evaporation; distillation	43
276		Japan, coastal waters	[(0.004-0.006)^{c}]	$Fe(OH)_3$-As_2S_3 coprecipitation; distillation; colorimetry	60
277	Silicon [H_4SiO_4; $H_3SiO_4^{-}$]	Adriatic Sea	[0.099(0.033-0.348)^{e}]	*See* reference 31	38
		Ionian Sea			
278		0-500 meters	[0.087(0.053-0.155)^{e}]		
279		650-1500 meters	[0.222(0.155-0.286)^{c}]		
280		Antarctic Ocean	[4.0]	Silicomolybdate colorimetry. *See also* references 138, 147.	26
281		Atlantic Ocean	[0.607(0.509-0.822)^{c}]	Ethyl acetate extraction of silicomolybdate in acid solution; colorimetry (335 mμ)	120
282		Narragansett Bay, R.I.	[0.128(0.121-0.135)^{b}]		
		Atlantic Ocean		*See* reference 2	105
283		100 meters	[0.028]		
284		950 meters, max.	[0.646]		
285		1500-4500 meters	[(0.477-1.07)^{c} [7]]		
		Cariaco Trench, Caribbean Sea			
286		100 meters	[0.132]		
287		800 meters, max.	[(1.68-2.02)^{c}]		
		Venezuela Basin, Caribbean Sea			
288		100 meters	[0.112]		
289		800 meters, max.	[(0.75-0.84)^{c}]		
290		1500-2500 meters	[(0.39-0.59)^{c} [7]]		
291		English Channel; North Sea; Pacific Ocean, off USA	[(0.02-3.0)^{c}]	Silicomolybdate colorimetry	142
		Gdansk Bay, Poland		Silicomolybdate colorimetry. *See also* reference 97.	96
292		February, 1958	[0.697]		
293		April, 1958	[0.424]		
294		May, 1958	[0.458]		
295		Indian Ocean	[0.515]	Silicomolybdate colorimetry	67
		Indian Ocean, N			114
296		Bottom	[(0.090-0.160)^{c}]	....	
297		Surface	[(0.002-0.005)^{c}]	....	
298		Thermocline	[(0.015-0.020)^{e}]	....	
299		Pacific Ocean, S, 0-100 meters: particulate	[(0.003-0.070)^{c}]	Membrane filtration; silicomolybdate colorimetry	25
300		Plymouth, England, offshore	[0.088 [12]]	Reduction of silicomolybdic acid with $SnCl_2$; Mo blue colorimetry. *See also* reference 2.	4

[7] Increases with depth. [12] Maximum observed in winter.

continued

191. NUTRIENT ELEMENTS IN SEAWATER

	Element [Probable Chemical State]	Source of Sample	Chlorinity Ratio g/unit Cl [Concentration, mg/L]	Analytical Method	Reference
301	Sodium [Na$^+$]	Bay of Bengal, inshore surface: Na$^+$	0.5641	Flame photometry	46
302		Pacific Ocean, NE: Na$^+$	0.5549	Gravimetric with zinc uranyl acetate	107
303		Puget Sound, Washington; Straits of Juan de Fuca, Canada & USA: Na$^+$	0.5562		
304		Tokyo Bay, Japan: Na$^+$	0.5554	....	78
305		Tokyo Bay, Japan: Na$^+$	0.5517	....	
306	Strontium [Sr^{++}; SrSO$_4$]	Antarctic Ocean	[0.104(0.101-0.108)[c] [1/]]	*See* reference 132	136
307		Indian Ocean	[0.099(0.093-0.104)[c] [1/]]		
308		Pacific Ocean, NW	[0.092(0.078-0.112)[c] [1/]]		
309		Atlantic Ocean: Sr^{++}	0.00042	Flame photometry; separation of Ca & Sr from H_2O	95
310		Atlantic Ocean: Sr^{++}	0.0005	Flame photometry	129
311		Atlantic, Arctic, & Pacific Oceans: Sr^{++}	0.00042 (0.00038-0.00046)[b]	Direct flame photometry	23
312		English Channel: Sr^{++}	0.000447	Activation analysis	14
313		Indian Ocean	[11.8]	Gravimetric as SrSO$_4$	67
314		Seto-naikai, Japan	[(7-8)[c]]	Ca removed by ion exchange; *o*-cresolphthalein complexone spectrophotometry	145
315		Plymouth, England, inshore waters	[(9-10)[c]]	Emission spectrography	12
316	Sulfur [SO$_4^{--}$]	Atlantic & Indian Oceans; Baltic, Mediterranean, & Red Seas (551 samples): SO$_4^{--}$	0.1395	Gravimetric with BaSO$_4$	139
317		Irish Sea: SO$_4^{--}$	0.13991 (0.13953-0.14029)[b]	Gravimetric with BaSO$_4$ after acidification with HCl	10
318	Vanadium [VO$_2$(OH)$_3^{--}$]	Atlantic Ocean, N; Heligoland, North Sea	[(0.002-0.0004)[c]]	Spectroscopy	36
319		Black Sea, surface	[0.00063]	Spectrography	152
320		Gullmarfjord, Sweden, shallow water	[<0.0005]	Optical & X-ray spectroscopy; chemical separation	93
321		Pacific Ocean, NW	[(0.0026-0.0035)[c]]	Fe(OH)$_3$-cupferron coprecipitation; phosphotungstate colorimetry	57
		Plymouth, England		Spectrography	12
322		Inshore	[(0.005-0.007)[c]]		
323		Offshore	[(0.0024-0.0027)[c]]		
324		Wakayama Prefecture, Japan	[(0.0034-0.0046)[c]]	Fe(OH)$_3$-cupferron coprecipitation; phosphotungstate colorimetry	62
325	Zinc [Zn^{++}; ZnSO$_4$]	Beaufort Channel, N.C., seasonal variation	[(0.0028-0.0146)[c]]	Dithizone colorimetry	18
		Gulf of Mexico		Activation analysis after coprecipitation	113
326		Ionic	[(0.0026-0.0064)[c]]		
327		Total	[(0.0056-0.0087)[c]]		
328		Gullmarfjord, Sweden, shallow water	[0.014]	....	93
329		Japan, offshore surface waters	[(0.0013-0.0015)[c]]	Dithizone colorimetry	89
330		Sagami & Suruga Bays	[(0.0018-0.0044)[c]]		
331		Misaki Channel; Tokyo & Ise Bays, Japan	[0.0056 (0.0028-0.0117)[c]]	Dithizone colorimetry	88
332		Plymouth, England, offshore; Scotland, west coast	[(0.009-0.021)[c]]	Spectrography	12

[1/] mg-atoms/kg.

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191. NUTRIENT ELEMENTS IN SEAWATER

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D. A. WOLFE and C. L. SCHELSKE, Radiobiological Laboratory, Beaufort, North Carolina. **Counting Efficiencies for Carbon-14 in Marine Productivity Measurements.**

Marine phytoplankton, labeled with C^{14} and collected on millipore filters, were counted with a gas-flow geiger counter, then combusted in oxygen combustion flasks. $C^{14}O_2$ was recovered with hyamine, and the absolute activities of the original samples were determined by liquid scintillation counting. Geiger counting efficiency, based on these absolute activities, was $25.8 \pm 1.19\%$. Intact filter papers containing C^{14}-phytoplankton also were counted directly by liquid scintillation, with an efficiency shown to approximate that obtained for soluble C^{14}-toluene added to the scintillation mixture as an internal standard. Liquid scintillation therefore appears to be a convenient and reliable substitute for geiger counting in productivity studies.

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PROGRESS IN BIOLOGICAL RESEARCH ON THE SURF CLAM, 1965

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(Abstract)

The Surf Clam Program is divided into two projects: (1) population dynamics, and (2) life history studies. Research in 1965 has contributed much along both lines of work to our understanding of the surf clam, *Spisula solidissima*.

Statistical information, current and historical, about the surf clam fishery has been gathered by port sampling, interviews, trips aboard commercial surf clam boats, and from records of major processors of surf clams. The relationship between shell length and wet meat weight was determined for surf clams collected off Point Pleasant and Cape May, New Jersey. Meats of Cape May clams were slightly heavier than those of Point Pleasant clams of the same shell length. Analysis of seasonal variation in meat quality proved it to vary with spawning condition.

Surf clam gonads have been collected for several seasons from New England to North Carolina. The spawning cycle for New Jersey clams is usually biannual; clams spawn in July and again in October. Sexual products are built up over the winter and gonads ripen in late spring.

Two extended surf clam biological cruises were completed in 1965. Nearly 600 stations were sampled with a modified commercial-type hydraulic jet dredge in an area of approximately 25,000 square miles extending from Montauk Point, Long Island, to Cape Hatteras, North Carolina. Bottom composition was noted and associated invertebrates were recorded or returned to the laboratory for later identification. Surf clams were measured (greatest overall length) to determine size composition of the populations. Salinities and temperatures were taken at the surface and bottom at each station. Surf clams were most abundant in the area of the present fishery off New Jersey. They were found in lesser numbers in a narrow band off the south shore of Long Island, New York, and offshore from Delaware Bay to False Cape, Virginia.

A population of small surf clams, less than 1 year old and under 1 inch long, was found in the inlet area of Chincoteague Bay, Virginia, in late 1964. This population has been closely studied and the changes in population density and growth of the small clams determined for 1965. Densities averaged about 20 clams per square foot over a 2-mile-long section of beach. Growth was about 2 mm per month but was somewhat slower during the winter. Observed mortality was high in 1965—the surf often cast windrows of clams upon the beach and moon snails and birds fed upon other small clams.

Studies of growth and population dynamics require a fast, permanent method of marking clams. A notch, ground into the surface and edge of the

valve with an electric hand tool, proved satisfactory. More than 43,000 small clams were marked; some were planted in the open sea off Chincoteague Inlet and others were planted in the outer part of Chincoteague Bay.

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REVIEW OF OYSTER CULTURE IN ALASKA, 1910-61

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ABSTRACT

There has been limited success with culture of the Pacific oyster, Crassostrea gigas *in the Coon Cove-Carroll Inlet area near Ketchikan since 1910. Since 1938 from 110 to 227 acres of tidelands have been leased yearly for oyster culture in this area. Several companies have participated at different times but the annual harvest has never exceeded 550 gallons of shucked meats.*

Culture of the Pacific oyster, *Crassostrea gigas* (Thunberg), may be practical under certain conditions in regions that are commonly regarded as unsatisfactory by oyster culturists in the continental United States (records available in the files of the U. S. Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska).

Seed oysters from Japan (obtained through the State of Washington Department of Fisheries or the Pacific Oyster Growers Association) were planted in areas extending from southeastern Alaska to Kachemak Bay on Cook Inlet at various intervals in 1910-61, but success was limited except in the Coon Cove-Carroll Inlet area near Ketchikan in southeastern Alaska. This area has proved moderately productive and has been a site of oyster culture for the past 50 years. Before 1937, tidelands were held by right of occupancy; in 1937-60 they were leased from the Federal Government under the Oyster Bottom Leasing Act; and beginning in 1960 the State of Alaska assumed responsibility for tideland leases. Acreages of tidelands leased are not available for all years, but it appears that from 110 to 227 acres have been used for oyster culture since 1938. Oyster production and acreage used for culture in the Coon Cove-Carroll Inlet area for 1940-61 are given in Table 1.

Celia Fairbanks and Judy Conkle were responsible for the first Alaskan plantings of Pacific oysters in George Inlet near Ketchikan in 1910. Oyster culture continued there and at Coon Cove and Carroll Inlet until 1920. Unfortunately, no details of this operation are available and records are lacking for the period 1920-38.

The Alaska Oyster Company leased tidelands at Coon Cove in 1938, and a year later marketed an unknown quantity of oysters. Because it takes as long as three years from seed to market size in this area, oysters planted prior to the 1938 lease date must have been cropped. About 300 acres were under lease in southeastern Alaska from 1938 to 1947, but oysters were produced on only 40 acres in Coon Cove and 100 acres at Shoal Cove, Carroll Inlet (also leased to the Alaska Oyster Company). They were sold on the local (Ketchikan) market. As no seed was imported from Japan from 1941 to 1947, the beds were nearly exhausted by 1945. Some seed oysters were planted in 1948, but none between 1949 and 1955. The Alaska Oyster Company went out of business in 1953.

The North Gem Oyster Company of Ketchikan leased 10 acres on the east shore of George Inlet in 1955 and added to their holdings each year until they held 247 acres in 1957. The company planted at the rate of 7,000 spat per acre in 1955, 5,500 per acre in 1956, and 28,600 per acre in 1957. In this 3-year period they harvested 100 gallons of shucked oysters, which probably represented a clean-up of some of the beds of the defunct Alaska Oyster Company.

In April 1955 the North Gem Oyster Company began an experiment with raft culture on the east shore of George Inlet opposite Beaver Falls — the only known trial of raft culture in Alaska. The experimental raft was made of eight cross-bars, each supporting 14 strings. The strings were

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TABLE 1. *Oyster Production, Coon Cove-Carroll Inlet Area near Ketchikan, Southeastern Alaska, 1940-61. (Asterisk indicates no data available; years with no data are omitted. Figures are from annual reports of area management agents.)*

Year	Company	Acres in production	Gallons (shucked)	Price per gallon
1940	Alaska Oyster Co.	140	*	$4.00
1941	-do-	-do-	82	3.50
1943	-do-	-do-	550	4.00
1944	-do-	-do-	500	4.00
1947	-do-	-do-	299	4.00
1948	-do-	-do-	114	6.00
1949	-do-	-do-	177	5.29
1950	-do-	-do-	0	—
1951	-do-	-do-	12	*
1956	North Gem Oyster Co.	110	100	*
1957	-do-	227	0	—
1960	Alaska Oyster Co.	227	100	*
1961	-do-	227	100	*

about 6 feet long and each held 11 or 12 seed shells. Buoyancy was provided by six empty 50-gallon oil drums. The 7,500 spat from Japan on the strings had attained an average length of 55 mm by September 11. Japanese seed usually is about 10 mm long when received for planting. Water temperatures ranged from 39° to 62°F during this period.

The same shipment of spat included 28,000 that were planted April 18 on 10 acres of nearby bottom. By September, losses were 3 per cent for the raft culture and 63 per cent for the bottom culture. The causes of mortality are unknown. Growth rates of two groups were reported by the company to differ considerably; the raft groups showed a much faster rate of growth. Oysters suspended from the raft attained lengths up to 160 mm (6.5 inches) in two years. No measurements are available for oysters grown on the bottom.

The North Gem Oyster Company went into receivership in 1958 and their holdings were taken over in 1960 by the newly formed Alaska Oyster Company, which immediately began to import seed and harvest oysters. During the winter of 1960-61 about 200 gallons of shucked oysters were sold locally. This company planted 700,000 spat on part of their holdings in 1960 and 2 million spat on 227 acres in 1961.

Two natural spawnings have been recorded in or near George Inlet. In 1939 a set was produced from natural spawning in George Inlet and a set occurred in Coon Cove in 1943.

Oyster culture was in progress in Alaska in 1961, but in a limited area near Ketchikan in southeast Alaska. Past attempts at oyster culture have been undertaken by undercapitalized companies with little experience. Well-planned and well-financed trials of Pacific oysters and introduction of the European oyster might expand the area of culture and increase oyster production.

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TUNA FISHING VESSELS, GEAR, AND TECHNIQUES IN THE PACIFIC OCEAN

By

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ABSTRACT

Tuna fishing vessels, gear, and techniques in the Pacific Ocean vary with the area and with the species sought. Tunas that live several hundred feet beneath the surface of the sea are taken across the entire breadth of the ocean by the longline technique, in which several hundred to over a thousand hooks are suspended from a line that may be over 50 miles long. The vessels of the longline fleet (largely Japanese) vary considerably in size; the largest are about 1,900 tons and have a range of 23,000 nautical miles. Often large mother ships are accompanied by a fleet of smaller craft. Tunas are caught in the surface and near-surface waters along the eastern and western shores and near islands. They are taken by three methods--pole-and-line fishing, purse seining, and trolling. Pole-and-line fishing is done near both the eastern and western shores of the ocean and near islands. The vessels are relatively small, except for a few in the eastern tropical Pacific. Large and highly mechanized purse seiners make the principal tuna catches in the eastern Pacific Ocean, although pole-and-line fishing and trolling also contribute to the landings.

INTRODUCTION

Longlining, purse seining, pole-and-line fishing, and trolling are among the important methods of fishing in the Pacific Ocean tuna fisheries. This report describes the vessels, gear, and techniques used in these methods of fishing as practiced in the Japanese and in the U.S. eastern Pacific and Hawaiian tuna fisheries.

The longline method is used in the Japanese winter fishery for albacore (Thunnus alalunga) in the North Pacific, the Japanese overseas (i.e., based in a foreign port) fishery for tuna in the South Pacific, and in Hawaii. Korean and Chinese vessels, which have recently entered the albacore fishery based at American Samoa in the South Pacific, have adopted the longline method as used by the Japanese. It was impractical or impossible to discuss all the different tuna fishing methods of the countries bordering or located in the Pacific Basin, or even to include all variations of the basic four. This report is based on the literature, and many of the fishing methods in various countries are not well documented.

Purse seine fishing for yellowfin tuna (Thunnus albacares) and skipjack tuna (Katsuwonus pelamis) in the eastern Pacific was not as successful during the early years of the fishery as pole-and-line fishing. Starting about 1957, however, and even before any major technological changes took place in the purse seine fleet, the catch per day of fishing of the purse seiners began to increase substantially. At the same time, several significant changes in equipment were being pioneered by progressive owners of a few vessels. These developments stimulated modernization or conversion of vessels for purse seine fishing by equipping them with power blocks, nylon seines, and improved fish-carrying facilities. The rate of conversion peaked about the middle of 1960. Almost all of the larger tuna clippers have now been modified for purse seining (Broadhead, 1962; McNeely, 1961).

In Japan, major fisheries for skipjack tuna and albacore depend on the pole-and-line method. Off the U.S. west coast substantial quantities of albacore are caught by pole and line. The pole-and-line method is used to catch skipjack tuna in Hawaii.

Trolling also is used to catch albacore in the U.S. west coast fishery. Albacore have been taken by purse seines, but large, tightly knit, slow-moving schools of albacore, which apparently are a requirement for profitable fishing with purse seines, appear infrequently off the U.S. west coast (Clemens, 1961).

LONGLINING

Japan

The Japanese longline vessels fish in almost all the world's warm seas. In 1941 the largest longliner was 150 gross tons and had a maximum cruising range of 5,000 nautical miles. Now longliners range up to 1,900 gross tons and have a cruising range of 23,000 nautical miles (Kanasashi, 1960).

Two types of boats are used for longline fishing. One is a vessel built specifically for the purpose and the other is a ''combination'' boat, which is built for pole-and-line fishing but is readily adaptable to longline fishing. The combination boat is described in the section on Japanese pole-and-line fishing.

Longline vessels are constructed of wood or steel; those of more than 100 gross tons are usually of steel. Most of the longliners are 250 to 350 gross tons; at this size they appear to be the most economical and efficient to operate. The general arrangement of a vessel of this class is shown in figure 1. The vessel diagrammed in figure 1 is 122.5 feet long at the waterline, and the beam is 22.31 feet. It is powered by a 550-horsepower diesel engine. The specifications of two typical longliners are given in table 1.

The layout of a larger--1,000 gross tons--longliner is shown in figure 2. It has a waterline length of 196.6 feet and a beam of 36.1 feet and is powered by a 1,500-horsepower engine. Boats larger than 1,000 gross tons carry one or more (up to six) catcher boats on each side of the deck. As the name suggests, catcher boats are built solely to catch fish and

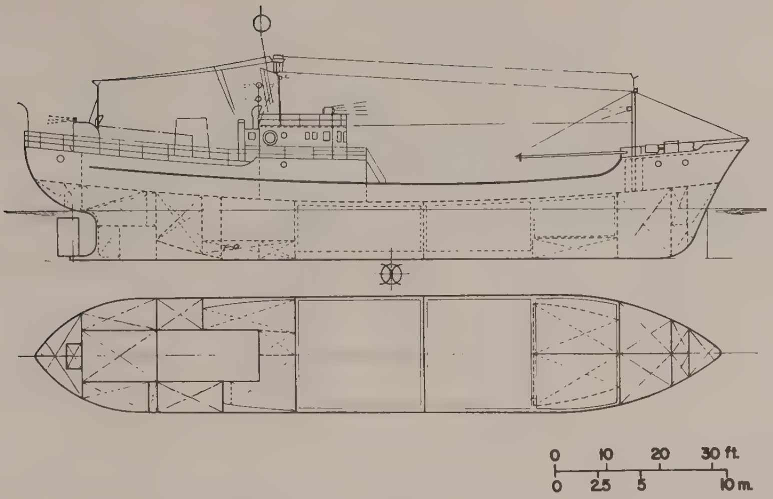

Figure 1.--General arrangement of 250-gross-ton Japanese tuna longliner (from Kanasashi, 1960).

Table 1.--Specifications of two typical longline vessels (from Kanasashi, 1960)

Specifications	Vessels	
	No. 1	No. 2
Gross tonnage	309.54	239.24
Year built	1958	1958
Length (ft.)	130	115
Beam (ft.)	24.6	22.3
Depth (ft.)	12	11
Capacity (cu. ft.):		
Fish hold	11,050	7,800
Fuel-oil tank	5,890	4,250
Fresh-water tank	911	530
Main engine (h.p. diesel)	650	500
Freezing capacity (tons/day)	6.5	1.9
Cruising range (nautical miles)	19,800	14,920
Weight of catch (tons)	170	116
Cruising speed (knots)	11.01	10.32
Crew:		
Deck	21	16
Engine	8	11
Clerk	2	1
Total	31	28

must depend on a mother ship for transport to the fishing grounds and for other support. Although catcher boats have a small fish hold, almost all the rest of the space is used to store fishing gear. Catcher boats are made of wood or aluminum (specifications of typical ones are given in table 2). Catcher boats can fish 200 to 250 baskets of longline gear. The mother ship stores the catches but usually does no actual fishing.

Longliners fish varying amounts of gear. Vessels of 39 to 99 gross tons fish 210 to 355 baskets; vessels 100 to 190 gross tons fish 355 to 400 baskets; and vessels 200 to 500 tons fish 400 to 450 baskets.

Longline gear is designed to fish about 500-600 feet below the surface of the sea. The basic unit of longline gear is the ''basket,'' a term which originated from the fact that at one time sections of the gear were stored in bamboo baskets. A basket consists of several sections of mainlines, either cotton or nylon, to which are attached a number of branch lines and a float line (fig. 3). Each branch line is composed of a length of cotton or nylon, a sekiyama (cotton thread wound around a core of wire), a

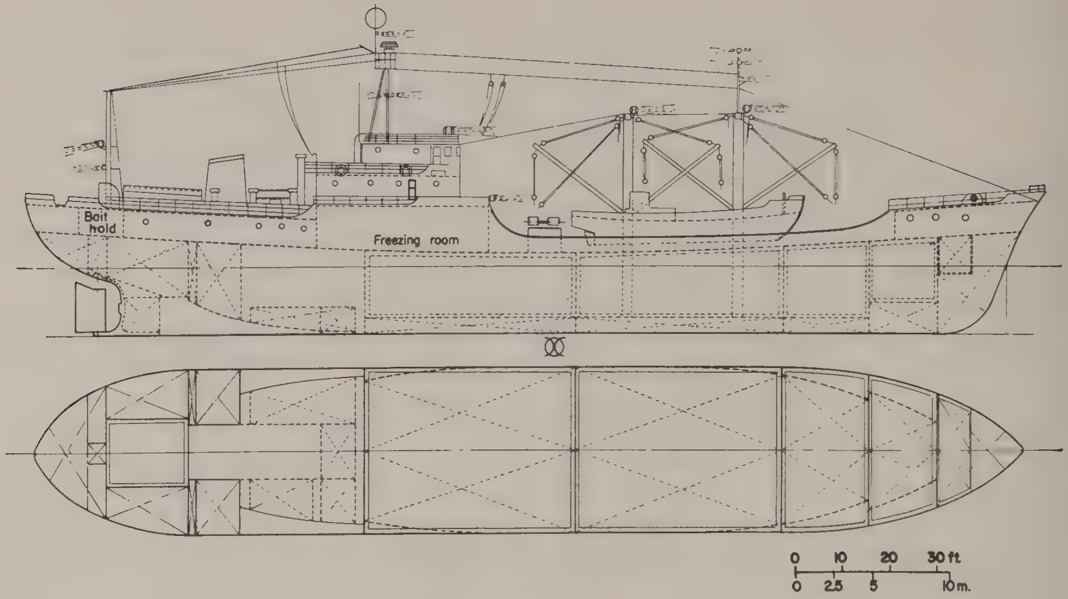

Figure 2.--General arrangement of a Japanese tuna longliner of 1,000 gross tons (from Kanasashi, 1960).

wire leader, and a hook. A swivel is often placed at the end of the cotton or nylon section of a branch line above the sekiyama to keep the branch line from twisting and tangling.

The baskets are tied in one continuous line when a set is made. Glass floats about 12 inches in diameter are used at all the basket junctures to buoy the set. The glass floats are tied to bamboo poles or light buoys which in turn are attached to the float lines.

Table 2.--Specifications of aluminum and wood longline catcher boats (from Kanasashi, 1960)

	Aluminum	Wood
Length (ft.)	46.5	52.5
Beam (ft.)	11.8	12.1
Depth (ft.)	5.25	5.4
Gross tonnage	19.8	19.5
Main engine (h.p. diesel)	75	90
Fish hold capacity (cu. ft.)	530	360

The longline is hauled in by a line hauler of the type shown in figure 4. This winch coils down the mainline automatically with little attention from the winch operator.

Mann (1955) described the hauling of the line as follows:

> "The coiling of the line is accomplished by the hauling head shown at the top of the winch. This assembly consists of a split sheave (A) grooved to fit the diameter of the line to be hauled; a wide center wheel with replaceable rubber collar (B); and a movable brass idler (C) controlled by the lever at the left. All three units are connected by a gear train which synchronizes them when they are

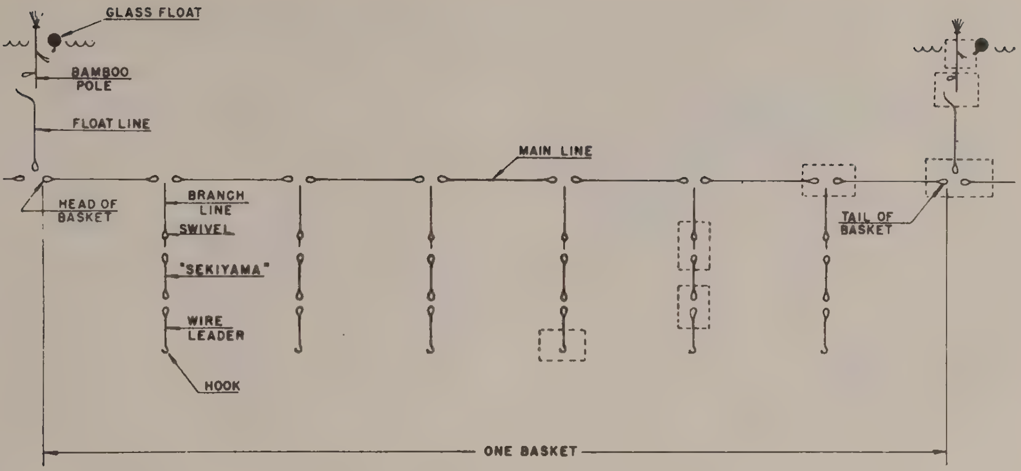
GLASS FLOAT
BAMBOO POLE
FLOAT LINE
MAIN LINE
HEAD OF BASKET
BRANCH LINE
SWIVEL
"SEKIYAMA"
WIRE LEADER
HOOK
TAIL OF BASKET
ONE BASKET

Figure 3.--Diagram showing components of a basket of longline gear (adapted from Shimada, 1951).

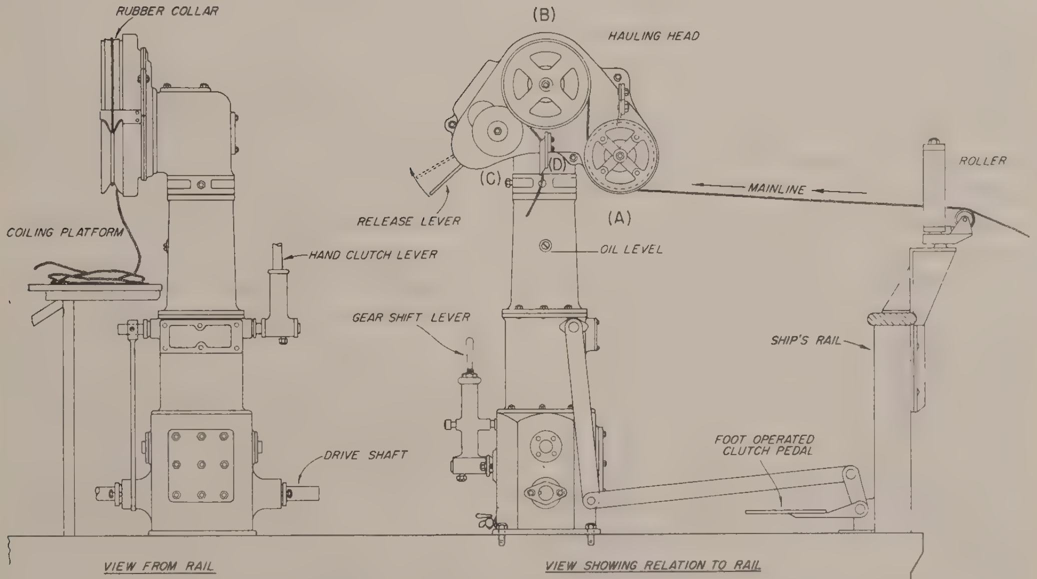
RUBBER COLLAR
COILING PLATFORM
HAND CLUTCH LEVER
DRIVE SHAFT
(B)
HAULING HEAD
(C)
(D)
RELEASE LEVER
(A)
OIL LEVEL
GEAR SHIFT LEVER
MAINLINE
ROLLER
SHIP'S RAIL
FOOT OPERATED CLUTCH PEDAL
VIEW FROM RAIL
VIEW SHOWING RELATION TO RAIL

Figure 4.--Japanese longline hauler (from Mann, 1955).

> turned by the drive shaft in the base of the winch.
>
> "In hauling, the incoming line is led under the grooved sheave, then over the center wheel and between it and the brass idler. The grooved sheave grips the line and the idler squeezes it against the rubber collar giving friction to pull the line in as the sheaves rotate.
>
> "The line is deflected downward by the brass plate (D) to a platform below, where it coils itself. The size of the coil is dependent upon the distance between plate and platform, so it is necessary to adjust the height of the latter with care.
>
> "The hauling head is turned by the drive shaft at the bottom of the winch through a multiplate oil-bathed disc clutch located in the base of the winch. The foot-operated clutch control is mounted near the ship's bulwark close to the overside roller so that the winch operator can see the incoming branch lines easily. The clutch control is so arranged that the winch operates continuously unless the clutch pedal is depressed.
>
> "The gear-shift lever shown at the lower left controls the hauling speed. With a drive shaft input speed of 300 r.p.m., high gear yields a line speed of about 1,000 ft./min., low gear a speed of 500 ft./min."

Japanese longline fishing can be either a single-vessel or multiple-vessel operation. Vessels in the 250-350 gross ton class appear to be most suitable for single-vessel fishing. They operate out of Japan or out of foreign bases.

The multiple-vessel operations can be classified by whether the mother ship carries catcher boats or services a fleet of boats that operate independently. Mother ships smaller than 1,000 gross tons are so arranged that they can tow a catcher boat from the stern; larger mother ships carry one or more catcher boats on deck (Kanasashi, 1960).

Mother ships that service regular longline vessels are often large. Vessels from about 3,000 to 11,000 tons have provided support for 23 to 50 catchers (Otsu, 1959). These catcher boats may range from the small boats carried on the deck of the mother ship to regular longline vessels used in single-boat operations.

The techniques of setting and retrieving longline gear have changed little over the years. The operation of a typical longline vessel, the Shiratori Maru, which participated in a mother ship operation, was described by Shimada (1951):

> "As is common practice among most long-line vessels, the baskets of long-line gear and floats aboard the Shiratori Maru were stowed behind the wheelhouse on the boat deck. Bamboo poles and light buoys were kept in racks located in the main deck passageways.
>
> "When ready to make a set, bait, either frozen sardines (Sardinops melanosticta), sauries (Colalabis saira), or both, was brought aft to the stern from the forward bait-storage hold. The work of assembling, baiting, and setting the longlines from the stern then commenced. /fig. 5./
>
> "MAN NO. 1 - Unties sling holding individual baskets together and slides loose baskets below on wooden table; also passes glass

floats to NO. 6; may be assisted by another man.

MAN NO. 2 - Shoves baskets along table and ties head of one basket to tail of another, thus joining baskets.

MAN NO. 3 - Uncoils float line which is on top of each basket, passes free end to MAN NO. 7, and stands by with remainder of coil; throws float line out when MAN NO. 7 lets float and pole overboard.

MAN NO. 4 - Frees tucked-in hooks from coils (leader and ' sekiyama ') and baits hooks.

MAN NO. 5 - Assists in baiting.

MAN NO. 6 - Ties glass floats to bamboo poles and passes poles to MAN NO. 7.

MAN NO. 7 - Receives end of float line from MAN NO. 3 and ties to bamboo pole with float attached; throws combination overboard at beginning of each basket in coordination with MAN NO. 3.

MAN NO. 8 - Throws out coils of main line.

MAN NO. 9 - Throws out bait hooks and branch lines.

MEN NOS. 10 and 11 - Break out bait from boxes and separate into individual fish, discarding poor ones.

MAN NO. 12 - Assists with bringing light buoys aft and tying on light buoys as required; renders general assistance and serves as relief.

''A basket of gear is set as follows: (1) the glass float and bamboo pole to which is tied the float line of the basket is thrown overboard to starboard as the vessel is under way; (2) the section of main line following the float line is cast directly astern; (3) a baited branch line is then cast to port and the main line following is cast to stern again. The procedure is repeated until the entire basket of gear has been laid. An extra float line and large marker flag is used to begin the first basket of a set and to end the last basket.

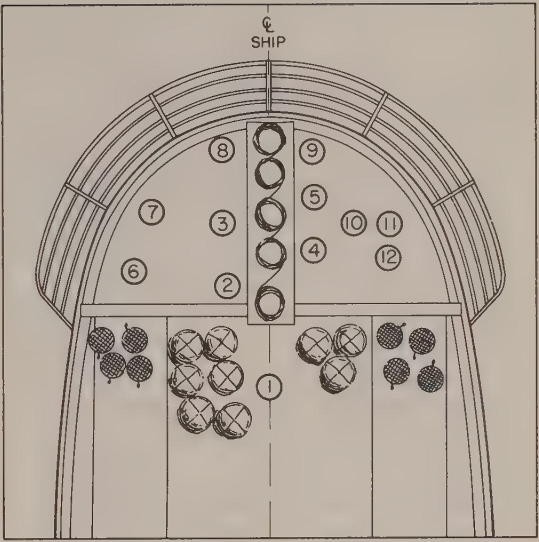

Figure 5.--Diagram showing usual positions of the fishermen when setting longline gear from the stern of the *Shiratori Maru* (from Shimada, 1951).

''Whenever possible gear is set along a straight course. The baskets are laid while the vessel is fully under way, the speed varying from 6 to 8 knots. The *Shiratori Maru* usually set 400 baskets of gear daily and required from 3-1/2 to 4 hours to get the lines into the water, an average of about half a minute being required per basket.

''Setting usually commenced before sunrise at about 3 a.m. and was completed by 7:00 a.m. at the

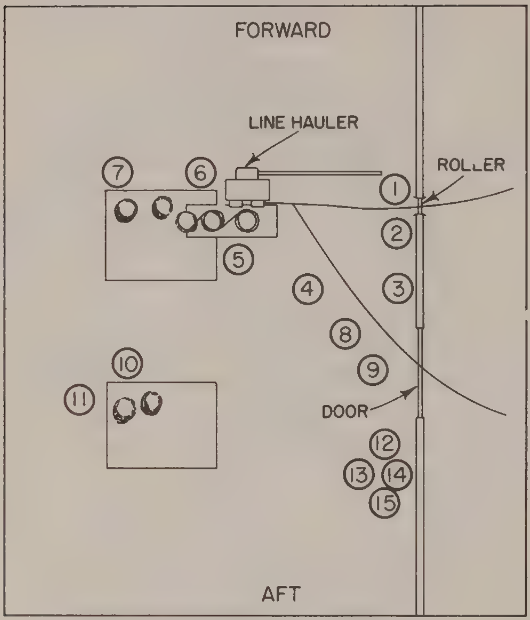

Figure 6.--Diagram showing usual positions of the fishermen when retrieving longline gear (from Shimada, 1951).

latest. The vessel then either drifted for several hours within sight of the flag marking the end of the set or headed back up the line of gear.

''When returning to the head of a set, a watch was continually kept to see whether fish had been caught on any of the branch lines. If there were signs of captured fish, the basket or baskets were taken in without untying them from the main set. The fish were removed, and the branch lines were rebaited and returned to the water.

''The laborious task of picking up the long lines usually started around noon and continued without stop until midnight. The average time required to bring in 400 baskets of gear was about 12 hours, but varied from 10 to 14 hours depending upon the number of fish that were caught.

''In picking up gear, the vessel was kept constantly under way at a speed of two to three knots. The necessary maneuvering required to maintain the ship at a 15°-45° angle to the main line required close coordination between the bridge and engine room, and a bell system was rigged between these two stations to expedite communications.

''The duties of individuals and sequences of handling /fig. 6/ are:

''MAN NO. 1 - Handles clutch of line hauler and regulates speed at which main line is taken in; watches direction from which main line is coming and guides man at wheel by hand signals.

MAN NO. 2 - Watches main line as it comes in and passes branch and float lines over roller to MAN NO. 3 as knots go through line hauler; adjusts roller to direction of line.

MAN NO. 3 - Coils leader and ' sekiyama ' and tucks hook around this coil, then coils part of cotton section of branch line and hands all to MAN NO. 4; also coils part of float line after bamboo pole and float have been removed.

MAN NO. 4 - Finishes coiling branch and float lines and gives coils to MAN NO. 6.

MAN NO. 5. Watches main line as it comes through line hauler and when section of main line between branch lines is coiled, moves coil from beneath line hauler toward MAN NO. 6; when branch line has been placed atop main line by MAN NO. 6, takes next section of main line already coiled and places atop branch line; repeats until basket is complete; unties tail of basket from head of next basket.

MAN NO. 6 - Takes coiled branch line from MAN NO. 4 and when section of main line has been moved from beneath line hauler by MAN NO. 5, places branch line atop this coil; coils float line, which is last attached line of basket to come in, and hands to MAN NO. 7.

MAN NO. 7 - Arranges coils of main line, branch lines, and float line in order, bundles basket together with a four-piece cotton rope sling and takes basket aft for stowage.

MAN NO. 8 - Pulls in bamboo pole and buoys; unties float line from pole.

MAN NO. 9 - Assists MAN NO. 8 in pulling in poles and buoys; removes glass floats.

MEN NOS. 10 and 11 - Rearrange baskets not properly coiled; tie in branch lines previously removed and replace worn leaders; assist MEN NOS. 2, 3, and 4 when necessary.

MEN NOS. 12, 13, 14, 15, and others - Bring in fish; gut and store catches; stow flags, buoys and gear; act as relief.

''The sequence in which a basket of gear is brought aboard is the reverse of that in which it is set; that is, (1) the main line is coiled as it comes aboard, and (2) a branch line is taken in and placed on top of the main line. This is repeated until all five branch lines have been retrieved. The basket is completed by bringing in the float line. The head of the basket is then untied from the tail of the next basket and the basket is bundled and stowed.

''Fish hooked on branch lines were brought in quickly by two or three of the crew members and gaffed when alongside. They were then pulled aboard through the door cut in the rail, killed if necessary, and immediately eviscerated if of a species other than yellowfin or albacore tuna. The landing of larger marlins and sharks frequently gave considerable trouble and, furthermore, tangled the lines badly. These fish, as well as any tuna which were taken alive, were killed by the fishermen who beat them on the head with large wooden mallets.''

Hawaii

Hawaiian fishing vessels and gear are based on Japanese models. The Hawaiian longline fishing boats evolved from the Japanese sampan-type live-bait boats (June, 1950). They are characterized by a high narrow bow, angular lines, a modified V-bottom, and moderate to low freeboard aft. They are usually constructed of wood. The length ranges from 28 to 62 feet overall. A typical boat is about 60 feet overall with a 12-foot beam and 6-foot draft.

Although details vary considerably, the general arrangement of the boats is similar to that shown in figure 7. Located slightly forward of amidships on the main deck is the pilothouse, which holds the radio equipment and steering and engine controls. A flying bridge, which may be completely enclosed or simply protected by a canvas windscreen, is frequently installed above the pilothouse and is equipped with additional steering and engine controls.

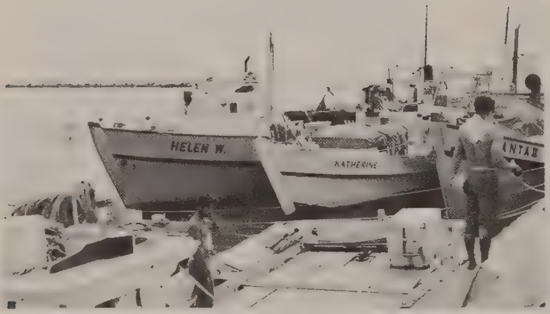

Figure 7.--Typical Hawaiian longline boats.

A raised trunk cabin, which generally provides storage space for fishing gear, is forward of the pilothouse. The engineroom, directly below the trunk cabin, houses the main engine, auxiliary generator, work bench, and fuel tanks. The high-speed diesel main engines vary from 115 to 165 horsepower. They drive a single screw through a reduction gear.

A structure, about 3 by 2 feet and 2-1/2 feet high, on the starboard side of the main deck, houses a gasoline stove for cooking. Forward of the engineroom, separated by a bulkhead, are sleeping accommodations for the crew. They consist simply of a tier of bunks. Abaft the engineroom, and separated by a bulkhead, is the fish hold, which continues aft to the water tank and lazaret. The fish hold consists of three compartments insulated along the sides and bottom with cork laid between the beams and covered with galvanized sheet metal. The total fish capacity of the hold is between 15,000 and 20,000 pounds. The boats are not equipped with mechanical refrigeration. The fish hold can be loaded with 25,000 to 30,000 pounds of ice to preserve the catch; this amount is considered adequate for a trip.

A spacious deck aft of the pilothouse facilitates handling the gear and landing large fish. A rack of two Y-shaped limbs on the aft bulwark on the starboard side provides storage for flag poles. The rudder post projects from the afterdeck and is provided with a socket for the insertion of a tiller. A plank rail completely around the main deck functions as a bulwark. A bin rail about 8 inches high extends along either side of the main deck about 18 inches inside the bulwark. The space between the bulwark and the bin rail ordinarily provides storage for the floats. It also serves as a temporary storage space for fish until they can be stowed below.

The technique of longline fishing was introduced to Hawaii from Japan. Therefore, the gear used by the Hawaiian longline fishermen is similar to the gear of Japanese longline fishermen, except for minor modifications to suit local conditions. The setting and hauling by the Hawaiian longline fishermen is also similar to that of the Japanese fishermen. The number of baskets fished by the Hawaiian fishermen, however, is far less than the number fished by the Japanese. The entire operation of a Hawaiian longline boat is a scaled-down version of the Japanese longliner operations. The Japanese longliner may fish a maximum of 400 baskets per set; the Hawaiian longliner sets a maximum of about 70 baskets. The lines are set between 5:30 and 7:00 a.m.; about 30 minutes to an hour is needed to set them. Hauling begins between 4:00 and 5:00 p.m. and is completed in about 3 to 4 hours. The average length of a trip is about 9 days and most of the trips are made within sight

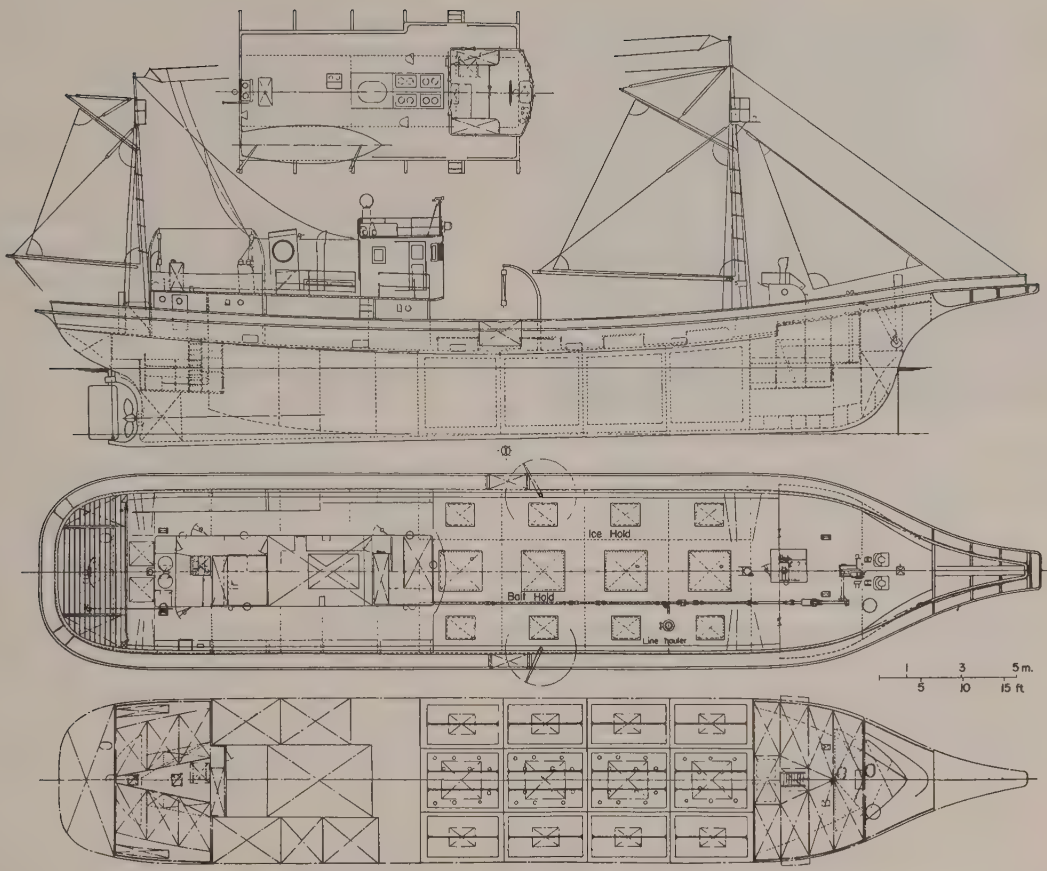

Figure 8.--General arrangement of Japanese pole-and-line boat (from Muramatsu, 1960).

of land (Shomura, 1959). The larger boats carry a crew of four or five but the smaller boats employ a crew of only two or three men (Otsu, 1954).

POLE AND LINE

Japan

Japanese pole-and-line tuna fishing boats have a long, high bowsprit (fig. 8). Fishing racks extend along one or both sides of the vessel, around the stern, and out along the bowsprit. The closely spaced nozzles of the spray system parallel the racks. The superstructure is abaft the beam. The long well deck has 9 to 12 hatches; the hatches along the midline open into the baitwells and those along the sides lead to iced fish holds. Specifications of some typical vessels are given in table 3. These boats are often termed ''combination'' boats because they are converted to longline fishing during the off season for pole-and-line fishing. Most of the wooden vessels range from 30 to 150 gross tons and the steel vessels from 150 to 180 gross tons (Muramatsu, 1960).

The fishing gear is composed of a bamboo pole 15 to 20 feet long, fitted with a hemp or cotton line 1 to 1-1/2 feet shorter than the pole. Jigs are composed of barbless hooks and various materials, including whale bone, bird feathers, and skins of fish.

Information on the location of fish schools is gathered by various means before the vessels leave port. Once on the fishing grounds, radio intelligence, visual observation, and trolling are relied upon to locate fish schools. Lookouts watch for bird flocks and floating timbers and other indicators of the presence of fish. Most vessels have a full-time radio operator whose principal duty is to obtain and relay reports on the fishing situation (Van Campen, 1960).

During fishing, members serve as chummers, bait carriers, or fishermen. The chummers usually are experienced fishermen. The bait carriers are less experienced fishermen who distribute live bait from the baitwells to the bait boxes for the chummers. On the fishing racks, the young skilled fishermen are stationed along the bowsprit where the lift is highest and the older or less skilled fishermen around the stern and along the side of the vessel. Chummers throw bait from the bow, stern, and amidships to attract the fish to the vessel.

Table 3.--Specifications of pole-and-line fishing boats (adapted from table 15, Muramatsu, 1960)

Ship's name	Myojyo Maru	Kotoshiro Maru	Kaio Maru	Choei Maru
Type of construction	Steel	Wood	Wood	Wood
Year launched	1948	1951	1949	1950
Principal dimensions				
Length (ft.)	101.4	97.8	81.4	74.8
Beam (ft.)	19.7	20.0	18.0	16.7
Depth (ft.)	10.2	10.3	9.2	8.0
Gross tonnage	159.8	153.2	97.9	78.0
Main engine (h.p. diesel)	320	430	210	210
Crew	65	70	57	50
Capacities (cu. ft.)				
Fish hold	5,141	5,552	3,581	3,147
Fuel-oil tank	1,639	1,519	816	619
Fresh-water tank	364	219	258	102

When a school of fish is detected the vessel moves toward it. If the situation looks favorable, live bait is chummed while the vessel moves slowly ahead. When the school rises to the bait, the boat stops with the fishing side, usually the port, to the leeward, and fishing begins (Muramatsu, 1960).

The sea-water spray system is turned on during fishing. The spray of water ruffles the surface of the sea and perhaps gives the illusion that the surface is alive with small fish. It is believed that this procedure improves fishing. The fishermen use one-pole rigs for fish up to 25 pounds; two-pole rigs are needed for larger fish. Jigs are used when the fish are actively biting; when the biting slackens, live bait is attached to barbless hooks.

Japanese pole-and-line vessels purchase live bait from bait dealers instead of losing potential fishing time in catching their own bait. Bait is purchased before putting out to sea. During the peak of the fishing season ''bait carriers'' (vessels which engage solely in the transport of bait) supply the fishing vessels on the grounds (Cleaver and Shimada, 1950). The most commonly used bait fishes are the anchovy (*Engraulis japonicus*) and the sardine (*Sardinops melanosticta*).

U.S. Eastern Pacific Tuna Fishery

The pole-and-line fishing fleet of the U.S. eastern Pacific tuna fishery is composed of (1) small (between 30 and 90 feet) bait boats which primarily fish for albacore in ''local'' waters and (2) larger boats (usually over 90 feet), better known as tuna ''clippers'', which range great distances in search of yellowfin and skipjack tuna. The large tuna clippers evolved from the small live-bait boat (fig. 9). The small boat is a flush-deck vessel with low freeboard aft, with the engine amidships or slightly forward, and with a large clear afterdeck on which stands the single bait tank (Godsil, 1938).

The modern tuna clippers, which range to 150 feet long, have raised decks forward running aft past amidships (fig. 10). Main decks are extremely low aft, and several raised wells are mounted on the stern to carry live bait. A canopy is built over the baitwells. Fishing is conducted from steel racks hung overboard from the bulwarks on the port side aft and around the stern (McNeely, 1961). Table 4 lists specifications of tuna clippers.

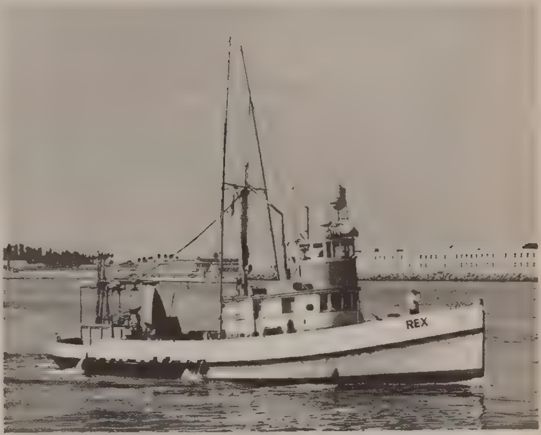

Figure 9.--Small pole-and-line boat used in the albacore fishery. (Photograph courtesy of California Department of Fish and Game.)

The gear consists of a bamboo pole with a hook at the end of a 6-foot line. The poles average between 8 and 9 feet long. The line is in two parts, a 2-1/2 to 3-foot length of heavy cotton line and a wire leader which bears the hook. Two types of hooks of various sizes are used. One is a plain galvanized barbless hook which is inserted through

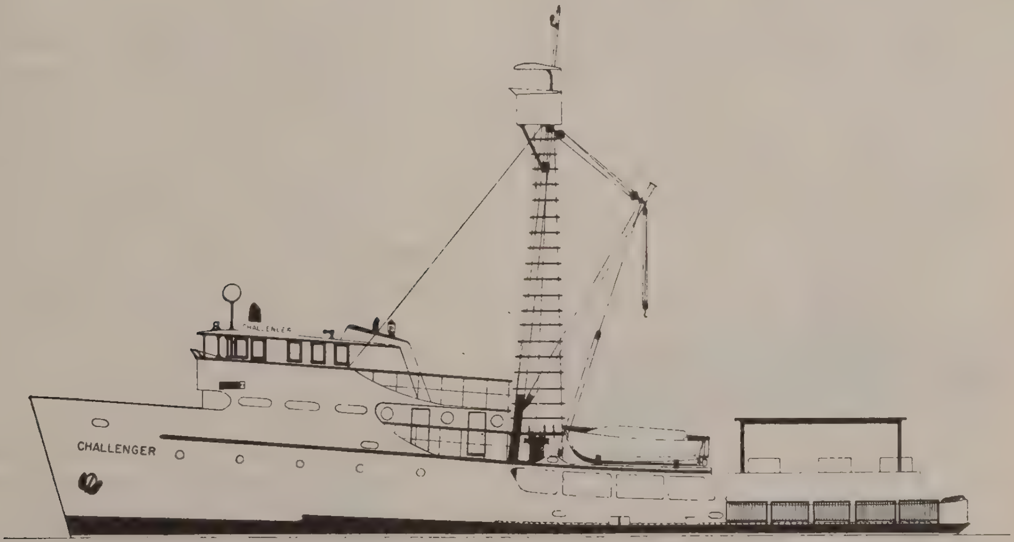

Figure 10.--Tuna clipper Challenger (from McNeely, 1961).

the back of the bait when fishing with live bait. The other is a similar hook with the shank embedded in tubular brass filled with lead and with feathers projecting beyond the hook. This is known as a squid or striker (Godsil, 1938).

For fish up to 20 or 30 pounds, each fisherman fishes with an individual pole. For fish between 30 and 50 pounds, a two-pole rig is used. Cotton lines from two poles are joined by swivels to a single leader and hook so that two fishermen are fishing the same line. For still larger fish three or more poles are attached to a single line (Godsil, 1938).

After a supply of bait has been obtained in inshore waters, the vessel proceeds to the fishing ground, where the crew scouts for tuna schools, as a rule visually. The presence of tuna may be detected by (1) fish leaping out of water, (2) a dark, ruffled spot in calm water, and (3) a flock of birds over a tuna school. Often a school of tuna is associated with porpoises.

When a tuna school is sighted the vessel moves toward it and live bait is thrown overboard to attract the fish to the vessel. When the tuna respond to the bait the engine is stopped, the crew clambers into the racks, and fishing begins[1]. As the fish strike indiscriminately at the lures or baited hooks and are hooked, they are jerked out of the water into the boat.

Table 4.--Specifications of tuna clippers (from Sundstrom, 1957)

Length (ft.)	68 to 150
Beam (ft.)	20 to 32
Draft (ft.)	8.6 to 15.4
Net tonnage	60 to 300
Construction	Steel or wood
Engine: type	Diesel
horsepower	250 to 1200
Type of refrigeration	Mechanical or brine tanks
Cruising speed	10 to 12 knots
Average crew	9 to 21
Length of trip	35 to 85 days

Several species of fish of the herring and anchovy families are used as bait. These fish occur in varying abundance in the bays and estuaries from southern California to northern Peru and around the Galápagos Islands. The most important species is the anchoveta (*Cetengraulis mysticetus*); others are the Galápagos sardine (*Sardinops sagax*), northern anchovy (*Engraulis mordax*), and California sardine (*Sardinops caerulea*) (Shimada and Schaefer, 1956).

Alverson and Shimada (1957) have described bait fishing as follows:

> "The clippers normally go into shallow areas, usually not more than 30 fathoms deep, to obtain bait although it is sometimes taken over deeper water and far offshore. Large encircling nets called 'lampara nets' are used to capture the baitfish. A clipper may carry several of these nets ranging in length from 80 to 150 fathoms. The size of the net used and some details of its construction depend upon the species to be caught and conditions on the baiting grounds.
>
> "The 'lampara net', which consists of two wings of large-mesh webbing on either side of a small-

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[1] Sometimes, depending on the behavior of the school, the vessel may keep moving with the school of fish while fishing is in progress (personal communication from Frank J. Hester, Bureau of Commercial Fisheries Tuna Resources Laboratory, La Jolla, California).

> mesh bag, is set from a large skiff which is towed around the school of bait by a power boat. The free end of the net is anchored by a small skiff during this operation. Then the circle is completed, the free end of the net is taken aboard the large skiff and both wings are pulled aboard so that the bag opens out and a shelf of fine-mesh netting is drawn under the fish. The small skiff is positioned to support the far side of the bag and the area of the net is reduced as the wings are pulled in. As the near edges of the bag are brought aboard the large skiff, the bait is completely enclosed in a small pocket of webbing. Depths permitting, the baitboat then comes alongside to take the baitfish aboard. Otherwise, the bait is transferred from the net into a collapsible live-bait box, called a 'receiver', which is towed out to the waiting clipper in deep water. There, the bait is loaded by means of small dipnets called 'scoops' into large tanks, or 'wells', through which sea water is circulated continuously.''

The small bait boats fishing for albacore may either capture all their own bait or purchase bait from live-bait fishermen before departing for the fishing grounds. Subsequently they may catch additional bait on the Baja California bait grounds. These vessels locate albacore schools primarily by trolling lures through the water. When an albacore strikes, the vessel is immediately stopped and the school is chummed with live bait. Meanwhile the trolling lines are secured and the fishermen start fishing with conventional pole-and-line gear (Clemens, 1955).

Hawaii

The Hawaiian skipjack tuna boats evolved from the Japanese tuna boats which were introduced to Hawaii around 1900 (June, 1951). Modifications in design have given rise to a distinct type of vessel with a high narrow bow and a moderate freeboard aft (fig. 11). The boats are about 50 to 80 feet long and have a beam of about 12 to 17 feet. They are generally of wood. A pilothouse and flying bridge is located amidships and live-bait wells (usually six) are fitted below the main deck abaft the engine room. A spray system composed of a series of nozzles spaced at 4-foot intervals extends across the stern and along the aft port and starboard gunwales. The catch is stored in the bait-wells as they are emptied of bait during fishing. The boats do not have mechanical refrigeration systems but some carry ice.

The fishing gear is similar to that used in other pole-and-line fisheries in the Pacific; it consists of a bamboo pole

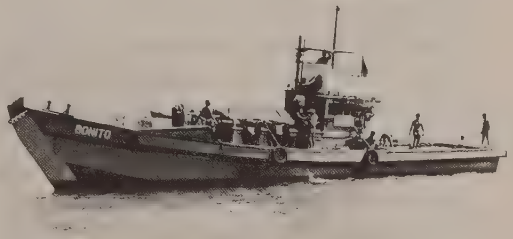

Figure 11.--Hawaiian pole-and-line boat.

to which is attached a length of line bearing a hook. The poles vary from 7.5 to 15 feet long. The shorter poles generally are used to catch fish over 20 pounds and the longer ones to catch smaller fish.

The jig used consists of a barbless hook, the shank of which is embedded in tubular lead or brass; variously colored feathers or threads are attached. A bit of dried fish skin or quill is fastened around the base of the feathers to prevent fraying. A plain hook with a live bait attached is used when the fish will not take a jig (June, 1951).

The Hawaiian fishermen rely mostly on bird flocks to locate fish schools. When a school is located the boat circles it in an attempt to cross ahead of it. As the boat approaches the school the engine is throttled down and the chummer begins to throw bait overboard, a few fish at a time. When the tunas respond to the bait, the chummer throws it more rapidly to bring the fish near the stern. The older and more experienced fishermen take their place along the stern of the vessel and the less experienced members take positions along the gunwales. The captain comes to the stern where he has a tiller to maneuver the boat while fishing is in progress (June, 1951).

The most important bait species is the small endemic anchovy with the local name of nehu (Stolephorus purpureus). The silverside or iao (Pranesus insularum) is another important bait fish. The Hawaiian fishermen spend a considerable amount of time in catching bait. Bait is caught during the day ("day-bait") and night ("night-bait") by two different methods. Lift nets, 15 to 25 fathoms long and about 12 fathoms deep, are fished at night. Surround (lampara) nets, generally about 50 fathoms long and 4 fathoms deep, but with a fairly deep bunt, are used during the day. The following account of baiting operations is from June (1951):

> "This gear /lift net/ is operated in combination with a submarine light which is used to attract the fish as the fishing boat lies at anchor over the bait grounds. The light is attached to the end of a pole and supported about 20 feet out from the port side of the boat. To prevent the light from splashing and possibly frightening the fish as the boat rolls, the globe is hung several feet below the surface of the water. The light is turned on about dark, and it is usually left on until about an hour before daybreak when a bait haul is made. If bait is especially plentiful, the net may be set whenever sufficient numbers of fish have been attracted by the light. Frequently, a rheostat is used to dim the light shortly before netting operations begin. This technique causes the bait to concentrate more compactly around the light, and it also serves to screen the movement of the net in the water. In making a bait haul, the net is paid out from the net skiff. One end of the cork line is secured to the port side of the stern of the fishing boat. The crew aboard the skiff pay the net out as the skiff is moved perpendicularly to the port side of the fishing boat. When the net is completely paid out, the skiff is turned parallel to the fishing boat, and the crew aboard the skiff then pull the lead line and

the rib lines as the skiff moves along the outer edge of the net. Meanwhile, aboard the fishing boat, the lead line is pulled from the bow and made fast, as are the rib lines. At a signal from the captain, the net is pulled on both the skiff and the fishing boat. As the net is 'dried up,' the fish are pocketed between the boat and the skiff. The light is turned out just before brailing begins, and the fish are transferred from the bag of the net to the baitwells aboard the fishing boat.

''A net skiff with an outboard motor attached is generally used for setting the surround net /for day-bait/ in waters over 1 or 2 fathoms deep. When a school of bait fish has been located, the net is paid out from the skiff as the skiff encircles the school. When the set is completed, the two ends of the net are pulled aboard the skiff. One of the fishermen holds the junction of the two ends of the lead line together to prevent the fish from escaping alongside the skiff, while five or six fishermen, wearing goggles, dive down and work the lead line over the bottom and thus keep the net from becoming snagged. When the net is sufficiently 'dried up,' the bait is brailed from the pocket of the net into a bait compartment built in the center of the skiff. The skiff then proceeds to the fishing boat where the bait is transferred to the baitwells. In the event that bait is caught close to the anchored fishing boat, the net with the captured fish is towed directly to the boat where the fish are brailed from the net into the wells. Since many of the baiting areas are over shallow coral-studded bottoms, it is often necessary for the fishing boat to anchor at a considerable distance from the scene of baiting operations.''

PURSE SEINING

U.S. Eastern Pacific Tuna Fishery

Almost all of the following description of the methods of fishing by purse seine is taken from the account by McNeely (1961).

Most of the purse seiners now fishing the high seas tuna of the eastern Pacific are converted tuna clippers or former U.S. Navy vessels. Their sizes range from 130 to 863 gross tons, and from 78 to 180 feet long.

The success of pioneering purse seiners that used the first all-nylon tuna purse seine and a mechanical device for power hauling of seines, the Puretic power block, triggered a large-scale conversion of tuna clippers and former naval vessels to purse seiners. Details of conversion vary, but essentially, it involves the removal of bait tanks, piping, circulation pumps, fishing racks, and accessory gear, leaving a clear afterdeck on which seine-fishing gear is installed. Figure 12 shows a tuna clipper after conversion to a purse seiner. Although most vessels require only slight, if any, modification to the basic hull structure, a few vessels with excessively sharp cruiser sterns may need sponsoning and broadening of the stern to accommodate the seine gear and increase stability. In earlier conversions, a turntable holding the net and skiff was placed on the cleared afterdeck. In later conversions, watertight

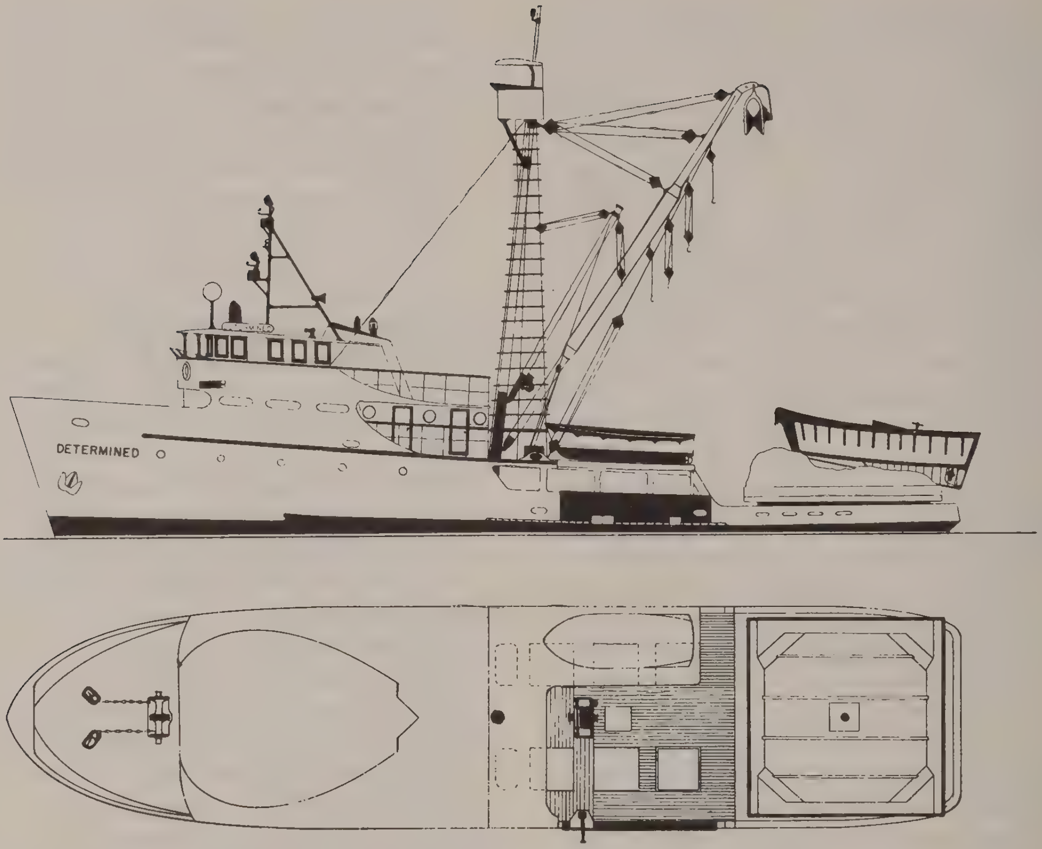

Figure 12.--Tuna clipper after conversion to purse seiner (from McNeely, 1961).

compartments were constructed directly under the turntables for increased buoyancy during bad weather. Still later innovations included the omission of the turntable altogether by substituing net platforms. On some vessels the upper deck is extended aft to the net platform, lower deck scuppers are sealed, and sides are constructed to enclose the lower deck.

It was necessary to replace the masts and booms of clippers with special masts and booms fabricated of double-strength steel tubes with diminishing diameters fitted one inside the other and welded at the external joints. The booms are long enough to extend to the stern rail, when lowered, and strong enough to lift the heavy seine as well as the seine skiff. High-pressure hydraulic lines running the full length of the boom from shipboard-mounted hydraulic pumps supply pressure to operate the power block.

Purse seining requires a heavy-duty winch with a minimum of three drums, two gypsies, and two heavy-duty lashing bits. Three drums are mounted on two parallel drive shafts that run fore and aft in the winch housing (fig. 13). The single purse line drum located on the port drive shaft holds about 600 fathoms of wire rope purse line. The purse line consists of sections, measuring 160 fathoms and 330 fathoms long, of 5/8-inch-diameter galvanized steel and a 110-fathom center section of 3/4-inch stainless steel wire rope. The two drums on the starboard drive shaft have independent drives and controls. The forward drum is used to haul in the bunt-end purse line, the after drum to hold about 200 fathoms of towing cable of 5/8-inch galvanized steel wire rope.

The majority of the purse seiners have turntables that measure about 25 feet by 25 feet. Table frames are built of heavy timbers and covered with 2-inch wood planking. Metal caps having guide grooves for the seine skiff are fitted over each end of the table to withstand wear. Supporting the table are eight or more roller-support pedestals of heavy-duty steel secured to the deck beneath the turntable. The table rotates on a center pin, which is usually made of two cast steel sections of about 8- and 9-inch-diameter, fitted one inside the other. One section is attached to the turntable and the other section to the deck.

Seine skiffs are usually made of plywood sheathed in fiber glass and plastic. A few are made of aluminum and stainless steel. The skiffs are large--about 20 feet long, 15 feet wide, and 4 feet deep. They are powered by 75 to 150 horsepower diesel engines. Powerful engines are needed because the skiff is used during fishing to tow the vessel and to maintain a steady pull to keep the vessel square with the net and to prevent it from being pulled into or drifting over the seine during pursing and hauling. A small rowboat or powerboat is carried in most seine skiffs to assist in pursing and other operations.

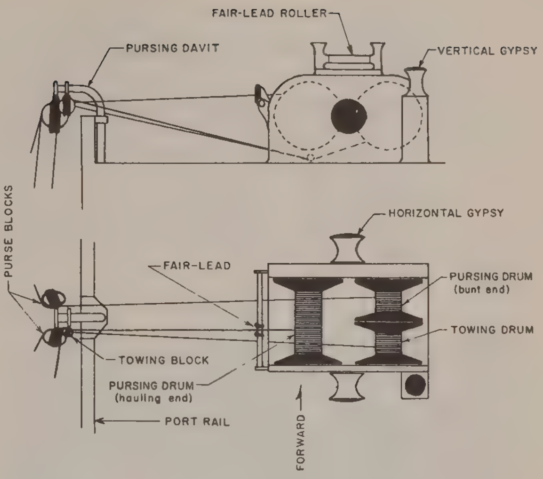

Figure 13.--Purse seine winch drum and cable arrangement (from McNeely, 1961).

Although minor variations exist, the design of purse seines is relatively standard (fig. 14). Typically the seine is approximately 425 fathoms long and 42 fathoms deep. The net is stacked in normal setting position on vessels not equipped with turntables. On vessels with turntables, the net is stacked in reverse order and the turntable is rotated 180 degrees to setting position.

Purse seiners use the same visual methods of locating tuna schools as tuna clippers. When a tuna school is sighted the purse seiner proceeds toward the school to make a set around it. In starting a set, the seine skiff is first lowered into the water, thereby creating a great amount of drag, which pulls the seine over the stern of the vessel into the water. The speed of the vessel in setting the net ranges from three-fourths to full throttle. A man in the mast (or an aircraft) directs the man at the wheel to make necessary changes in direction

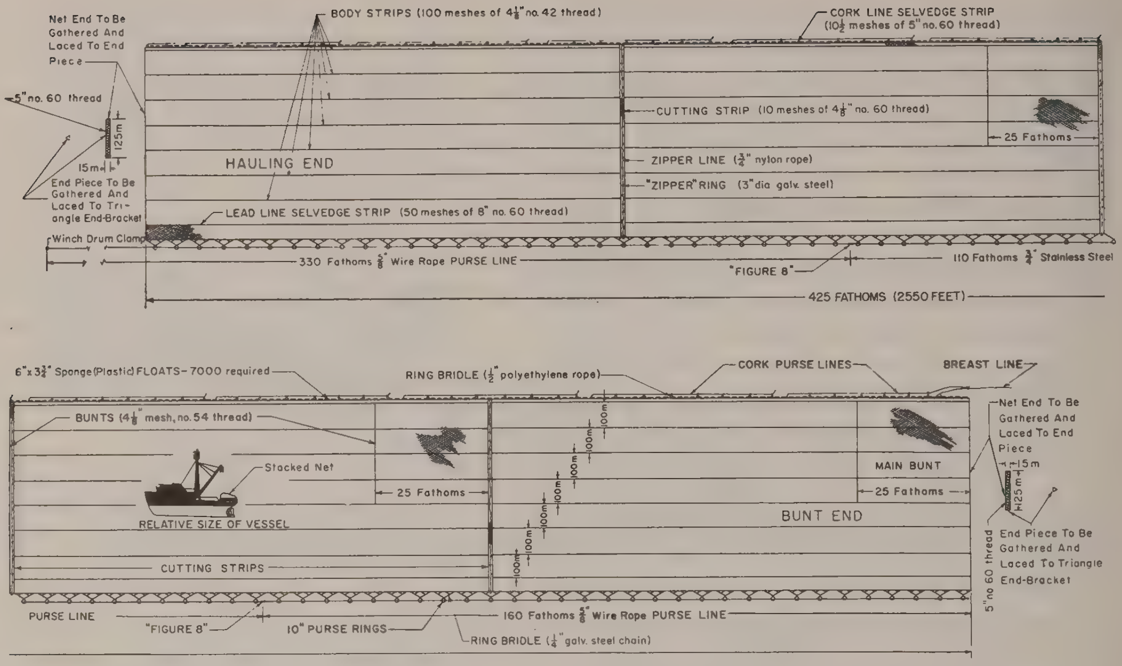
Net End To Be Gathered And Laced To End Piece
5" no. 60 thread
125m
15m
End Piece To Be Gathered And Laced To Triangle End-Bracket
Winch Drum Clamp
BODY STRIPS (100 meshes of 4⅛" no. 42 thread)
HAULING END
LEAD LINE SELVEDGE STRIP (50 meshes of 8" no. 60 thread)
330 Fathoms ⅝" Wire Rope PURSE LINE
CORK LINE SELVEDGE STRIP (10½ meshes of 5" no. 60 thread)
CUTTING STRIP (10 meshes of 4⅛" no. 60 thread)
25 Fathoms
ZIPPER LINE (¾" nylon rope)
"ZIPPER" RING (3" dia galv. steel)
"FIGURE 8"
110 Fathoms ¾" Stainless Steel
425 FATHOMS (2550 FEET)
6" x 3¾" Sponge (Plastic) FLOATS - 7000 required
RING BRIDLE (½" polyethylene rope)
CORK PURSE LINES
BREAST LINE
BUNTS (4⅛" mesh, no. 54 thread)
Stacked Net
RELATIVE SIZE OF VESSEL
25 Fathoms
CUTTING STRIPS
100m
100m
100m
100m
100m
100m
MAIN BUNT
25 Fathoms
BUNT END
Net End To Be Gathered And Laced To End Piece
15m
125m
End Piece To Be Gathered And Laced To Triangle End-Bracket
5" no. 60 thread
PURSE LINE
"FIGURE 8"
10" PURSE RINGS
160 Fathoms ⅝" Wire Rope PURSE LINE
RING BRIDLE (¼" galv. steel chain)

Figure 14.--Construction details of tuna purse seine (from McNeely, 1961).

to afford the most advantageous positioning of the net around the school of fish.

Four methods of control are practiced to prevent the fish from escaping before the pursing is completed: (1) use of ''cherry bombs'' (small explosives), (2) running the net skiff or auxiliary speedboat between the opening of the net and the stern of the purse seiner, (3) hammering on the side of the vessel with a sledge hammer or on the side of the skiff with a smaller hammer, and (4) flashing an underwater light between the purse lines during pursing in night hauls.

As the purse seiner approaches the net skiff, after encircling the school of fish, the vessel is brought to a stop near the seine skiff. At this point the bunt end of the net is transferred from the skiff to the vessel. The seine skiff then proceeds to maneuver to control the fish as described above. As soon as the opening between the ends of the net is closed, the skiff proceeds to the starboard side of the vessel, where a towing line is attached. The skiff then throttles at full speed to keep the purse seiner square with the net.

Aboard the vessel the other necessary operations to complete the set are carried out, including pursing, ''drying up,'' and restacking the seine. Hauling and stacking of the seine continue until the area occupied by the fish becomes minimal. At this time, the skiff releases the towing line from the vessel and proceeds to pick up the cork line of the seine, thus forming a pocket between the skiff and the vessel. The net is ''dried up'' further by strapping aboard sections of the bunt webbing by the use of a power winch. Brailing begins after the fish are brought to the surface in a compact bag.

TROLLING

U.S. West Coast Albacore Fishery

There apparently is no "typical" albacore trolling vessel. The albacore fishery includes vessels of myriad sizes, shapes, and descriptions (Clemens, 1955). Trolling boats are almost always of wood, but any small- to medium-sized boat, from 16-foot skiffs to boats 60 feet long, may be used (fig. 15). The majority are about 35 to 45 feet long (Scofield, 1956). When salmon trolling is not very productive many salmon trollers from California, Alaska, British Columbia, Washington, and Oregon fish for albacore farther south. The salmon trollers, which are easily convertible to albacore trolling, are 25 to 60 feet long and have a beam of 8 to 18 feet. They are mostly of wood, are 5 to 26 net tons, and have diesel or gas engines rated from 25 to 165 horsepower (Sundstrom, 1957).

The outrigger poles are usually constructed of douglas fir, hemlock, or eucalyptus, and are 25 to 60 feet long. Bow poles, when used, are about 20 feet long. Poles taper from 4 to 5 inches in diameter at the butt to about 2 inches at the tip. The poles extend from each side of the vessel and may be as low as horizontal during fishing[2]. When not fishing, the poles may be swung up to the vertical along the mast by means of hinged sockets attached to the butt end of the poles. The poles serve to spread the attachment of the fishing lines farther out than the beam of the vessel (Scofield, 1956).

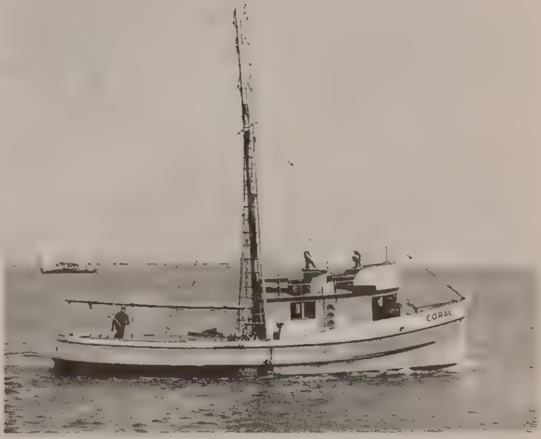

Figure 15.--Albacore trolling boat. (Photograph courtesy of California Department of Fish and Game.)

To absorb the shock when a fish strikes, a shock absorber of rubber or spring is fastened between the pole and the tag line. The tag line, which may also be called pole line, brail line, shock line, drag line, or standing line, facilitates the detachment and storage of the trolling lines. The length of the tag lines varies with the position on the outrigger pole and is as long as the distance from the attachment at the pole to the place on the stern gunwale where the lines are secured when the boat is not fishing. The aft end of the tag line is provided with a swiveled snap fastener to hold the mainline. An inhaul line is attached to the snap.

The mainline is hard-laid cotton of 72 to 108 thread, which is usually dyed dark blue or green. Hemp rope (sometimes tarred) and twisted nylon sometimes may be used. The leader is composed of monofilament nylon, braided dacron, or some other synthetic material. A short piece of wire, 2 to 6 feet long, is placed just forward of the lure

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[2] The angle from the horizontal to which the poles are lowered while fishing appears to vary widely. The angle may be as great as 30° to 45° above the horizontal. (Personal communication from Richard L. McNeely and Frank J. Hester.)

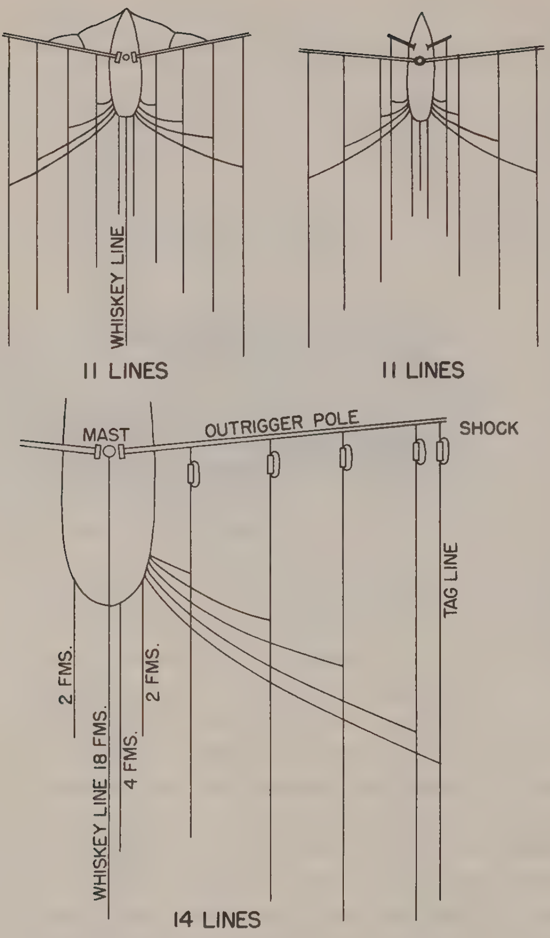

Figure 16.--Diagrammatic drawing of the arrangement of lines for three different albacore trolling boats (from Scofield, 1956).

to prevent the teeth of the fish from cutting the leader. The total length of the leader is 4 to 20 feet; the average is 18 feet[3].

Lures are made of plastic, bone, feathers, and artificial squids, to which are attached single or double barbless and barbed hooks.

In addition to the lines attached to the poles, several lines are usually attached to the stern of the boat. The total number of lines trolled by a boat varies, but averages about 11. The length of the lines, exclusive of the tag lines and leaders, ranges from 3 to 15 fathoms. The longest line is positioned at the tip of the pole and each line toward the base of the pole is progressively shorter (fig. 16).

Trolling involves simply the dragging of a line with lure behind a moving boat. Trolling for albacore is usually done at an average vessel speed of 6 knots. The lines are trolled near the surface and fish are usually hauled in by hand.

ACKNOWLEDGMENTS

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[3] Lines and leaders fabricated of synthetic material are now being used extensively by trollers in the San Diego area. Nylon lines obviate the use of shock absorbers and wire leaders have been almost eliminated. (Personal communication from Frank J. Hester.)

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Swimming Speeds of Yellowfin and Skipjack Tuna

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ABSTRACT

Five hundred ten measurements of swimming speeds of skipjack tuna (*Euthynnus pelamis*) from four schools and 33 of yellowfin tuna (*Thunnus albacares*) from one school were made from underwater motion-picture records obtained at sea. The relation of swimming speed to rate of tail beats is described for yellowfin averaging 51.9 cm long and for skipjack averaging 57.2 cm long. At similar rates of tail beats, yellowfin swam faster than skipjack when speed was measured in body lengths per second. Variations in the mean swimming speed of the schools of feeding skipjack were unrelated to body length. The difference between the swimming speeds of tunas observed during this study, which ranged from 0.5 to 14.4 body lengths per second (0.3 to 6.9 m per second), and higher speeds previously reported for tunas is discussed.

INTRODUCTION

The pelagic existence of scombrid fishes makes it difficult to measure their swimming speeds. It places the researcher in a position of attempting to measure the speed of an object from a ship which is itself moving. One important difficulty introduced by ship's motion, disregarding the possible personal plight of the observer, is measuring the relevant components of movement of a ship far from any fixed point of geographic reference in order to get the true speed of the fish. In addition, irregularities of the sea surface combined with the schooling nature of scombrids make it a rare occasion that a single fish can be observed long enough to measure its swimming speed.

A variety of methods, which ignore or overcome some of the difficulties, has been used by various investigators for measuring swimming speeds. Watanabe (1942) timed skipjack tuna (*Katsuwonus pelamis*) as they swam a marked distance of 2 m alongside a ship. The use of a bicycle speedometer attached to a rod and reel to measure the speed of a 60-pound tuna caught on a hook is reported by Lane (1941). A rod and reel were used also by Walters and Fierstine (1964) but with a higher degree of technological sophistication, to measure the swimming speeds of yellowfin tuna (*Thunnus albacares*). They used a magnetic tape recorder to register the speed at which a fish pulled a line carrying evenly spaced iron particles and then analyzed their records with an oscilloscope. An ultrasonic pulse sonar was chosen by Nishimura (1963) to measure speeds of yellowfin, albacore, and bluefin tunas. By measuring swimming speeds of captive Pacific bonito (*Sarda chiliensis*) feeding in a large oval tank, Magnuson and Prescott[1] circumvented the difficulties connected with observations at sea. They obtained speeds from underwater motion pictures in a manner patterned after the method described in this report. Kishinouye (1923), Kramer (1960), and Barsukov (1960) have also reported on the swimming speeds of tunas but they did not describe their methods. When the diversity of techniques is considered, it is not surprising that the swimming speeds reported should range from 0.8 to 25 m per second.

The present paper describes swimming speed and tail-beat frequencies for skipjack tuna (*Euthynnus pelamis*) and yellowfin tuna (*T. albacares*) from underwater motion pictures of feeding schools at sea.

MATERIALS AND METHODS

In 1958 the Biological Laboratory of the Bureau of Commercial Fisheries, Honolulu, began experiments at sea as part of a study on the feeding behavior of skipjack. Observations were made from the research ship, M/V *Charles H. Gilbert*, which is equipped with an underwater viewing chamber on the portside near the stern (described in Strasburg and Yuen, 1960). Live bait was used as chum to attract the tuna into viewing range.

Motion-picture records of the tuna pursuing live bait near the ship were the source of data for the calculations of swimming speed. Three schools of skipjack were photographed in July and August 1959 in Hawaiian waters. A school of skipjack and one of yellowfin provided more data in April 1960 near Roca Partida, off the coast of Mexico.

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[1] Magnuson, John J., and John H. Prescott. (MS) Courtship, locomotion, feeding, and miscellaneous behaviour of Pacific bonito (*Sarda chiliensis*). Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii.

The activity of the fish was recorded on 16-mm color film. The camera was hand-held with its lens flat against the pane of the window in a fixed position at right angles to the keel of the ship. The skipjack near Hawaii were photographed at 24 frames per second as the ship moved forward at approximately 2 knots. The skipjack and yellowfin at Roca Partida were photographed at 48 frames per second while the ship was stationary. To obtain an accurate measure of the frames per second on the last two schools a clock with a second hand was photographed for 10 seconds on each roll of film.

Fish were caught from each photographed school. Fork lengths were measured for specimens taken randomly from the catch of each school. Temperatures were read from a continually recording thermograph.

Movie sequences which recorded fish swimming in a plane approximately parallel to the window were selected for analysis. Fish were considered to be in this plane if their images showed little or no change in size during the sequence. The progression of the fish from frame to frame was followed by marking the positions of tip of snout and fork of tail of each clear image on a screen of tracing paper on a Craig film editor. When the Roca Partida films were analyzed the method was improved by using a Recordak Library Film Reader (Model C) instead of the film editor.

Tail beats of the selected fish were counted to the nearest ½ beat. A tail beat is defined as the complete cycle from the start of a beat through to a return to the starting position. Tail beats could be counted only from sequences taken at the high speed of 48 frames per second.

The patterns of movement of the fish obtained from the films included the effects of the rolling, pitching, and in some cases forward motions of the ship. Effects of yawing were considered to be negligible because of the method of selecting sequences for analysis. Corrections were made for the vertical component of motion caused by the rolling and pitching when the ship was stopped and also for the horizontal component when the ship was moving forward. No correction was made for the angular component of pitching.

Correction for vertical displacements consisted of realignment of the images. A straight line was drawn through the points representing the head and tail of the penultimate image. The head and tail points of the final image were then copied onto a second sheet of paper overlaid on the first. This second sheet was moved vertically until the tail point of the final image fell on the line of the penultimate image. The positions of the head and tail of the penultimate image were then marked on the superimposed sheet which again was vertically adjusted until the tail point of the penultimate image fell on the line of the preceding image. The procedure was continued until the first image in the sequence was incorporated onto the adjusted path. The number of images used per sequence ranged from 2 to 15 (4 was most frequent).

After alignment, the distances between successive positions of the tip of the snout were measured; the average of the two body lengths bordering each distance served as the unit of measure. Average speed was calculated by adding the distances between positions and dividing by time in seconds. Measurement of the distance in small portions in the above manner made possible the correction of the slight differences in image size resulting from changing distances between fish and camera.

To correct the combined effects of the forward and rolling motions of the ship, the successive positions on the film were first determined as has been described. At this point the true distances between the positions of the fish had to be calculated. The basis for this calculation is shown in Figure 1. Here the successive positions of the fish on the film are A and E, the points that determine LM, the path of movement. It is known, however, that the fish actually had moved farther along LM because the ship was moving forward (to the right in the figure) along a line parallel to NO. The distance traveled by the ship (EC) is laid out along NO and a perpendicular to NO is erected at C. The intersection B is the estimated position. If the fish is swimming in a direction opposite that of the ship, the same broad procedure holds, but C falls between A and E. The position of B need not be determined geometrically. Once angle a is established, the length of the segment EB can be computed as EC secant a.

In practice, the computations are simplified if the distance AE is converted into speed and EC made to represent the speed of the ship.

Finally, the average speed for the entire distance was obtained by calculating the weighted mean of the speeds within individual time intervals.

The speed of the ship for each school was estimated by taking one-half of the difference between the average uncorrected speed of fish swimming toward the stern and of those swimming toward the bow. This step is valid, of course, only if the mean swimming speeds of fish in the two groups are the same. Only those fish which were swimming in line with a horizontal plane should have been used for this estimate but, because so few individuals met this criterion, the angular limits were extended to 20 degrees from the horizontal to obtain an adequate sample. Since fish other than those swimming in the horizontal plane were used, ship's speed was estimated by a two-step process. A first estimate was obtained from the uncorrected swimming speeds of the fish. The swimming speeds were then corrected with this first estimate of ship's speeds. The once-corrected swimming speeds were then used to refine the initial estimate of ship's speed.

Speed is expressed in body lengths per second because the technique used in acquiring the data actually measured the distance traveled by a fish only in terms of its length. The expression of speed in relative units may be preferred to absolute units in view of the results of Bainbridge (1958) who found that the relation between swimming speed and rate of tail beat was the same for dace, trout, and goldfish 3.6 to 29.3 cm long if swimming speeds were expressed in body lengths per unit of time.

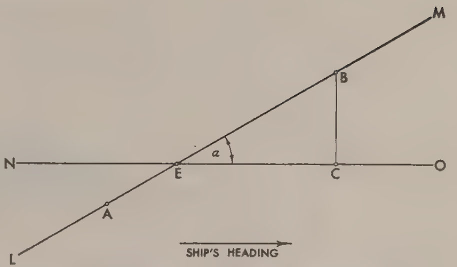

FIGURE 1.—Diagram to explain procedure used to correct swimming speeds for the effect of ship's speed. Explanation in text.

The mean lengths of fish caught from each of the four skipjack schools and one yellowfin school are listed in Table 1 together with other information. The duration of observations ranged from 0.1 to 2.2 seconds. Eighty per cent of the observations lasted 0.1 to 0.7 second.

RELATION OF SWIMMING SPEED TO RATE OF TAIL BEATS

The relation of swimming speed to the rate of tail beats was determined for the yellowfin and skipjack schools encountered near Mexico. The relation for skipjack (Figure 2) is expressed by the following equation, fitted by least squares:

$$S = 2.053 + 0.479T,$$

where S represents the swimming speed in body lengths per second and T is the number of tail beats per second ($s_t = 1.888$, $s_s =$

TABLE 1.—*Information on observations of swimming speed*

Date of photography	Location		Species of tuna	Mean fork length (cm)	Water temperature (C)	Estimated ship's speed (meters per second)
12 July 1959	21°18′ N	158°18′ W	Skipjack	64.35 ± 3.47	26.6	0.3
25 July 1959	22°22′ N	157°22′ W	do	79.19 ± 5.21	26.2	0.6
14 August 1959	21°10′ N	157°55′ W	do	48.31 ± 1.42	26.1	1.0
23 April 1960	19°00′ N	112°04′ W	do	57.20 ± 4.96	23.9	0.0
23 April 1960	19°00′ N	112°04′ W	Yellowfin	51.86 ± 3.56	23.9	0.0

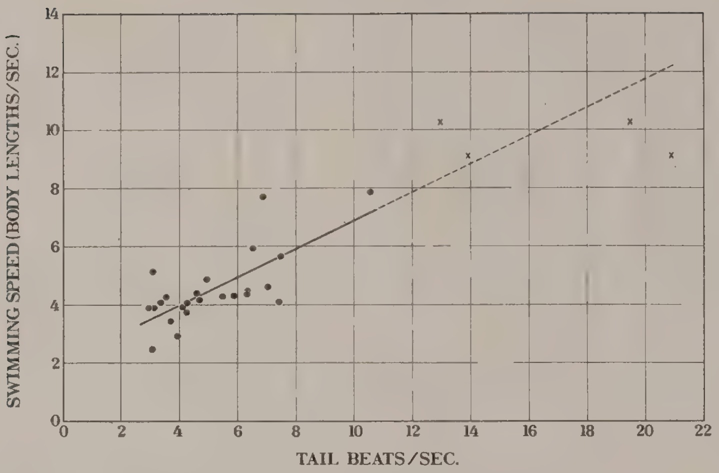

FIGURE 2.—Relation of swimming speed to rate of tail beats for skipjack tuna.

1.248, $s_{s.t} = 0.880$, $n = 24$, 95% confidence interval for the slope b is 0.277–0.680). The four x's in Figure 2 represent high and low tail-beat counts of two skipjack which were swimming too rapidly for accurate counting. They are included in the figure to show that extrapolation of the line to about 10 body lengths per second would not be unreasonable. Calculation of regression did not include these points.

For yellowfin the relation between swimming speed and tail-beat rate (Figure 3) is expressed by:

$$S = 2.446 + 0.567T$$

($s_t = 2.744$, $s_s = 2.265$, $s_{s.t} = 1.674$, $n = 33$, 95% confidence interval for b is 0.347–0.788).

For both skipjack tuna and yellowfin tuna the relation between swimming speed and tail-beat rate should not be extended beyond the limits of the observations. Extrapolation to the

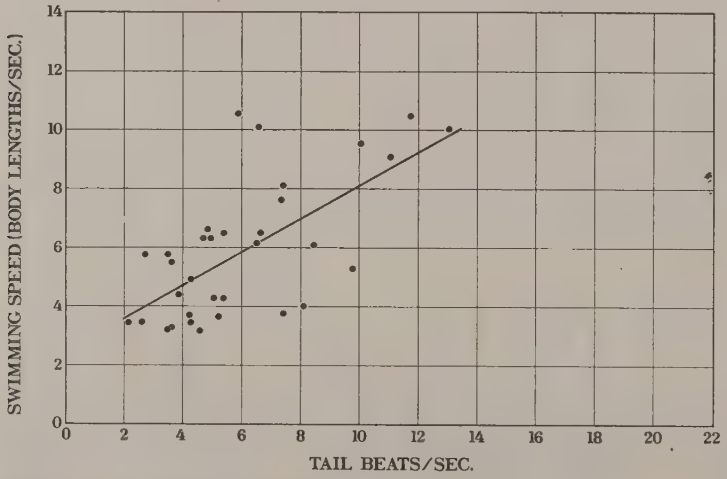

FIGURE 3.—Relation of swimming speed to rate of tail beats for yellowfin tuna.

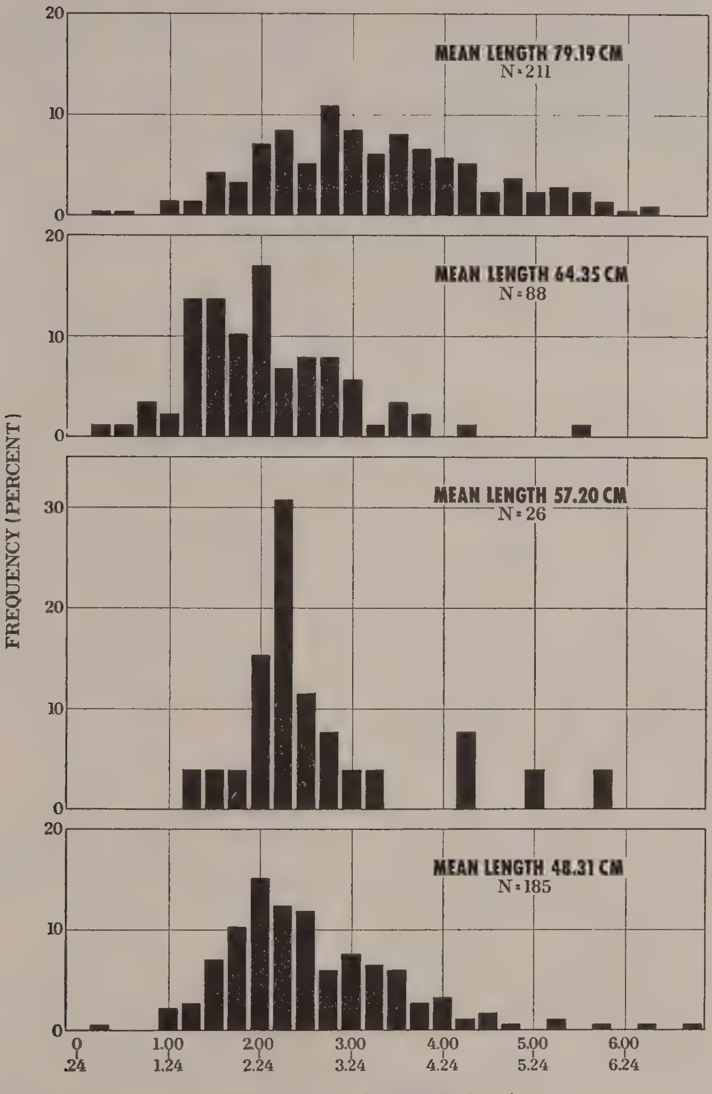

FIGURE 4.—Frequency distributions of swimming speeds of skipjack of various sizes in four schools.

left would imply that these species are capable of moving forward at a speed greater than two body lengths per second without moving the caudal fin. Observations of swimming skipjack and yellowfin indicate no other fins are used in a manner which would produce forward motion. As with dace (*Leuciscus leuciscus*), trout (*Salmo irideus*), and goldfish (*Carassius auratus*)—see Bainbridge (1958)—the linear relation between swimming speed and rate of tail beat probably changes at lower tail-beat rates because of variations in the amplitude of the beat.

The mean length was 57.2 cm for the individuals in this skipjack school and 51.9 cm for those in the yellowfin school. An "*F*-test"

(Snedecor, 1956) was used to compare the mean swimming speed expressed in body lengths per second and adjusted for tail-beat rate. The speed of the yellowfin was significantly greater than that of the skipjack at the 5% probability level ($F = 5.25$, $F_{P.05} = 4.02$). This difference indicates that 52-cm yellowfin travel a greater portion of their body length per tail beat than do 57-cm skipjack, which is contrary to the findings of Bainbridge (1958).

These tunas, moreover, swim faster at the the tail-beat rates measured than do the dace, trout, and goldfish of Bainbridge's experiments.

VARIABILITY OF SWIMMING SPEED OF FEEDING SKIPJACK TUNA OF FOUR SCHOOLS

The four schools of skipjack observed represented a range in mean fork length of 48.3 to 79.2 cm (Table 1). The frequency distributions of speeds, as converted into meters per second by applying mean body lengths as conversion factors for the four schools (Figure 4) were compared by applying the nonparametric median test (Siegel, 1956). The resulting Chi-square of 59.92 ($p < 0.001$, 3 degrees of freedom) indicates that the speeds of the various size groups were not drawn from the same population.

It is apparent from Figure 4, however, that although a relation between size and swimming speed per tail-beat rate may exist, the swimming speeds of feeding skipjack are determined by factors other than size. In skipjack, whose reaction to food stimuli includes an increase in swimming speed, variations in swimming speed among feeding schools probably reflect to some extent different levels of feeding motivation.

COMPARISON OF PRESENT AND EARLIER FINDINGS

The swimming speeds of yellowfin tuna, 1.6 to 5.4 m per second, measured in this study fall between other reported speeds of 1 to 1.5 m per second (Nishimura, 1963) and 5.2 to 20.7 m per second (Walters and Fierstine, 1964) for yellowfin. In reporting the relatively slow speeds, Nishimura (1963) did not specify the activity of the yellowfin, which were swimming as deep as 120 m. In view of the findings on Pacific bonito by Magnuson and Prescott (MS—see footnote 1), who noted that bonito swam faster when they were feeding or courting, it is possible that the speeds of feeding yellowfin tuna measured in this study are greater than Nishimura's measurements because of a difference in kind of activity.

The speeds of 1.6 to 5.5 m per second for yellowfin tuna reported here are smaller than those reported by Walters and Fierstine (1964) by a factor of 3.6 on the average. The difference may be attributed in part to difference in the nature of the activity of the fish and in part to the difference in size. They measured speeds of yellowfin tuna 53 to 98 cm long struggling at the end of a hook. If the swimming speeds are expressed in body lengths per second, the difference between 6 to 21 body lengths per second for yellowfin in distress and 3 to 10 body lengths per second for feeding yellowfin seems reasonable.

The swimming speeds of feeding skipjack tuna—a range of 0.3 to 6.9 m per second and a mode at 2.0 to 2.2 m per second are much lower than the previously reported 5 to 10 m per second (Watanabe, 1942) and 11 m per second (Kishinouye, 1923). The difference is inexplicable with present information.

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THE EFFECT OF TEMPERATURE UPON THE GROWTH OF LABORATORY-HELD POSTLARVAL PENAEUS AZTECUS

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Bureau of Commercial Fisheries, Galveston, Texas

THE EFFECT OF TEMPERATURE UPON THE GROWTH OF LABORATORY-HELD POSTLARVAL PENAEUS AZTECUS[1]

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The general life-history of North American shrimp of the genus *Penaeus* has been known for some time (Weymouth, Lindner and Anderson, 1933; Pearson, 1939; Burkenroad, 1934). Adults of the white shrimp, *P. setiferus,* the most intensely studied species, spawn offshore. The young move to the estuaries and, after a period of rapid growth, return to the offshore spawning grounds. During the estuarine phase of the life cycle, the postlarvae, and later the juveniles, are exposed to wide variations of temperature and salinity. Although it has been suggested that the lower salinities of the estuaries are necessary to the growth and survival of these postlarval penaeids (Pearse and Gunter, 1957; Gunter, Christmas and Killebrew, 1964), recent laboratory studies indicate that salinity *per se* has little effect on growth of postlarval *P. aztecus* (Zein-Eldin, 1963).

Zein-Eldin and Aldrich (1965) suggested that temperature was of greater significance than salinity for growth and survival of *P. aztecus.* Their experiments were, however, conducted at only four temperatures: 11°, 18°, 25°, and 32° C. The resulting data indicated greater differences in growth rate between groups held one month at 11° and 18° C. or those at 18° and 25° C., than between groups held at 25° and 32° C. The greatest growth-differential per 7 degrees was between 18° and 25° C.

As a result of these experiments, we decided to make a more exhaustive study of the effects of temperature in the range (15°–35° C.) commonly encountered by the postlarvae.

METHODS

Postlarval *P. aztecus* were obtained from the surf zone of the Gulf of Mexico at the entrance to Galveston Bay and kept in the laboratory for 24 hours before introduction into experimental aquaria. Postlarvae were tested at five constant temperatures in each of two series. In Series 1, we tested at temperatures of 15° through 25° C. at intervals of 2.5°, and in Series 2, temperatures of 25° through 35° C. at the same intervals. Animals were obtained for Series 1 in April, 1964, from water of about 23° C., and for Series 2 in August, 1964, from water of about 29° C.

Groups of 20 postlarvae were placed in glass aquaria containing 4 liters of continuously aerated and filtered bay water (salinity approximately 25‰). Five such aquaria, prepared as described by Zein-Eldin (1963), containing a total of 100 animals, were held in darkness at each constant temperature in B.O.D.-type

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[1] Contribution No. 216, Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas.

TABLE I

Mean animal weight (mg.) and length (mm.) at each temperature level (°C.)
Values are based on samples of 10, except where indicated. Figures in parentheses indicate one standard error

Temperature	Series 1									
	15°		17.5°		20°		22.5°		25°	
Elapsed time (days)	Mean length (mm.)	Mean weight (mg.)	Mean length (mm.)	Mean weight (mg.)	Mean length (mm.)	Mean weight (mg.)	Mean length (mm.)	Mean weight (mg.)	Mean length (mm.)	Mean weight (mg.)
0	12.0 (0.3)	5.1 (0.2)	12.0 (0.2)	5.1 (0.2)	12.0 (0.2)	5.1 (0.2)	12.0 (0.2)	5.1 (0.2)	12.0 (0.2)	5.1 (0.2)
5	12.2 (0.3)	5.2 (0.4)	12.0 (0.2)	7.0 (0.4)	12.4 (0.3)	8.2 (0.3)	12.6 (0.3)	9.0 (0.7)	13.5 (0.3)	12.2 (0.7)
10	12.7 (0.2)	7.4 (0.5)	12.4 (0.3)	8.7 (0.7)	12.8 (0.4)	10.5 (1.2)	13.5 (0.3)	14.7 (1.2)	14.6 (0.8)	29.1 (4.1)
14	11.8 (0.3)	7.0 (0.8)	12.6 (0.3)	9.6 (0.7)	13.9 (0.5)	15.2 (1.4)	16.7 (0.6)	30.0 (1.2)	18.4 (1.0)	49.9 (9.6)
20	12.0 (0.2)	7.4 (0.4)	13.2 (0.5)	12.8 (1.5)	16.6 (0.6)	28.2 (3.0)	18.9 (0.6)	43.8 (3.8)	22.6 (2.0)	90.2 (18.3)
25	12.2 (0.2)	7.9 (0.5)	14.4 (0.2)	15.2 (0.8)	19.1 (0.9)	43.3 (6.1)	21.2 (0.8)	64.7 (7.5)	28.5 (0.9)	158.7 (13.6)
31 Sample of 10	12.7 (0.3)	9.6 (0.8)	15.0 (0.3)	17.6 (1.4)	20.8 (0.6)	50.9 (4.4)	24.3 (1.2)	97.2 (7.0)	34.0 (1.3)	264.3 (33.2)
All survivors	12.6 (0.2)	9.8 (0.5)	14.5 (0.2)	16.7 (0.8)	20.7 (0.3)	52.2 (2.9)	23.9 (0.6)	90.6 (2.9)	33.0 (0.8)	241.7 (18.4)
No. of survivors	30		37		44		41		29	
No. of artificial deaths	2		2		5		7		19	
No. removed for sampling	52		50		50		51		49	
	Series 2									
	25°		27.5°		30°		32.5°		35°	
0	9.4 (0.1)	3.6 (0.2)	9.4 (0.1)	3.6 (0.2)	9.4 (0.1)	3.6 (0.2)	9.4 (0.1)	3.6 (0.2)	9.4 (0.1)	3.6 (0.2)
5	10.4 (0.2)	5.4 (0.6)	10.9 (0.3)	6.7 (0.6)	11.6 (0.3)	8.7 (1.0)	11.4 (0.4)	8.5 (1.0)	10.6 (0.2)	7.0 (0.7)
11	13.4 (0.4)	16.3 (1.2)	15.9 (0.6)	29.1 (2.8)	17.0 (0.5)	35.5 (3.3)	16.4 (0.7)	33.4 (4.0)	10.9 (0.2)	7.4 (0.5)
15	16.0 (0.3)	33.0 (2.2)	20.5 (0.7)	57.5 (6.0)	21.5 (1.0)	72.2 (8.8)	19.6 (0.9)	55.5 (6.6)	11.2 (0.4)	8.7 (1.1)
20	21.0 (1.3)	65.5 (8.9)	21.8 (1.6)	76.8 (15.2)	25.0 (1.2)	108.4 (14.2)	25.3 (1.0)	113.6 (13.9)	—	—
25	24.7 (0.9)	101.9 (12.2)	25.1 (1.7)	124.6 (18.5)	31.0 (1.7)	224.6 (35.8)	29.0 (1.7)*	199.4 (36.7)	—	—
29 Sample of 10	27.2 (1.0)	140.4 (13.6)	31.2 (1.9)	230.7 (32.7)	32.2 (2.6)	272.9 (46.0)	34.0 (1.7)	299.6 (47.5)	—	—
All survivors	26.4 (0.4)	125.6 (6.2)	30.5 (1.2)	219.8 (20.4)	32.3 (1.8)	265.8 (32.1)	34.0 (1.7)	299.6 (47.5)	—	—
No. of survivors	37		30		15		10		0	
No. of artificial deaths	5		7		14		19		30	
No. removed for sampling	50		50		50		45		20	

* Sample of 5.

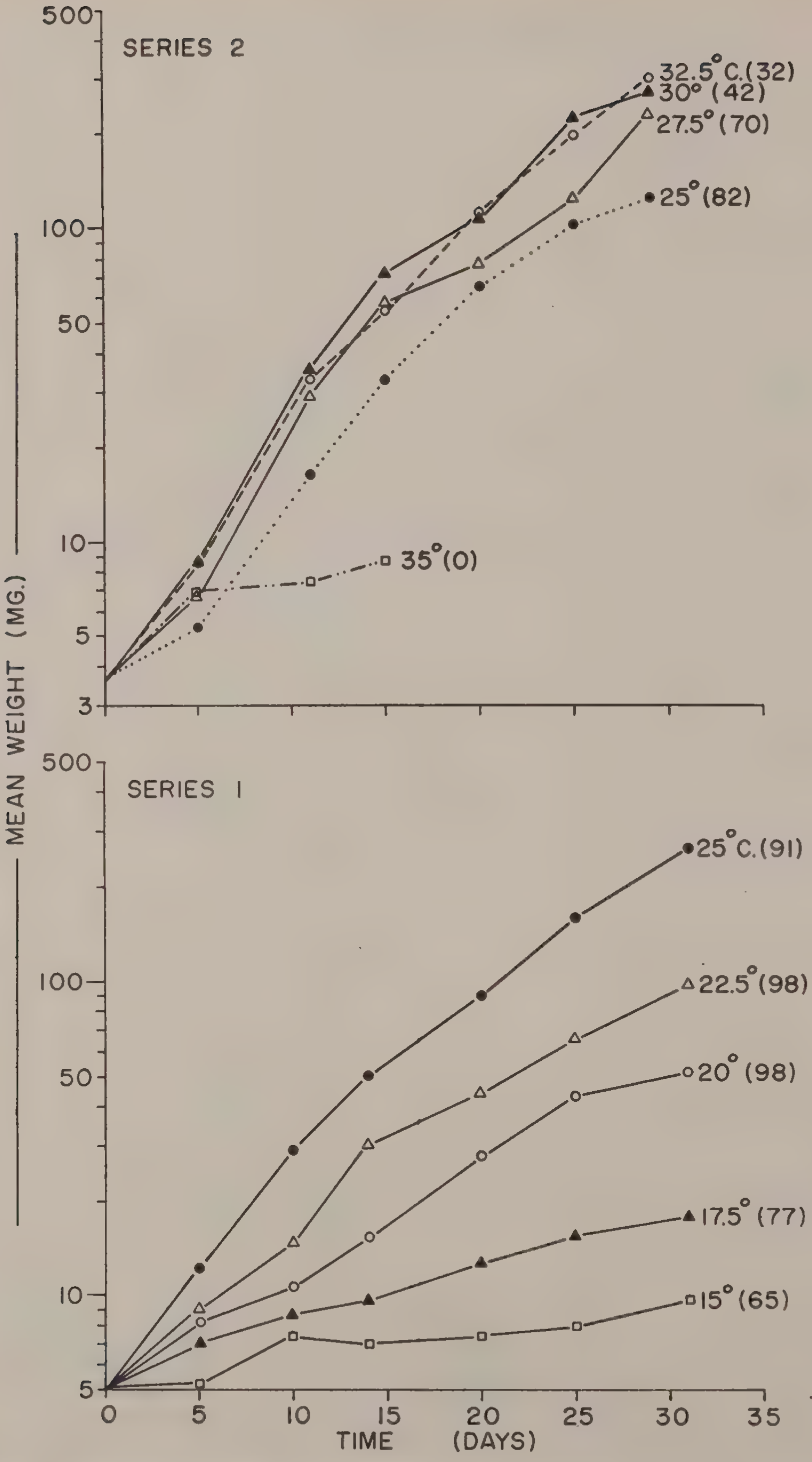

FIGURE 1. Mean increase in weight of *P. aztecus* postlarvae exposed to different temperatures (°C.) for one month. Figures in parentheses indicate per cent survival.

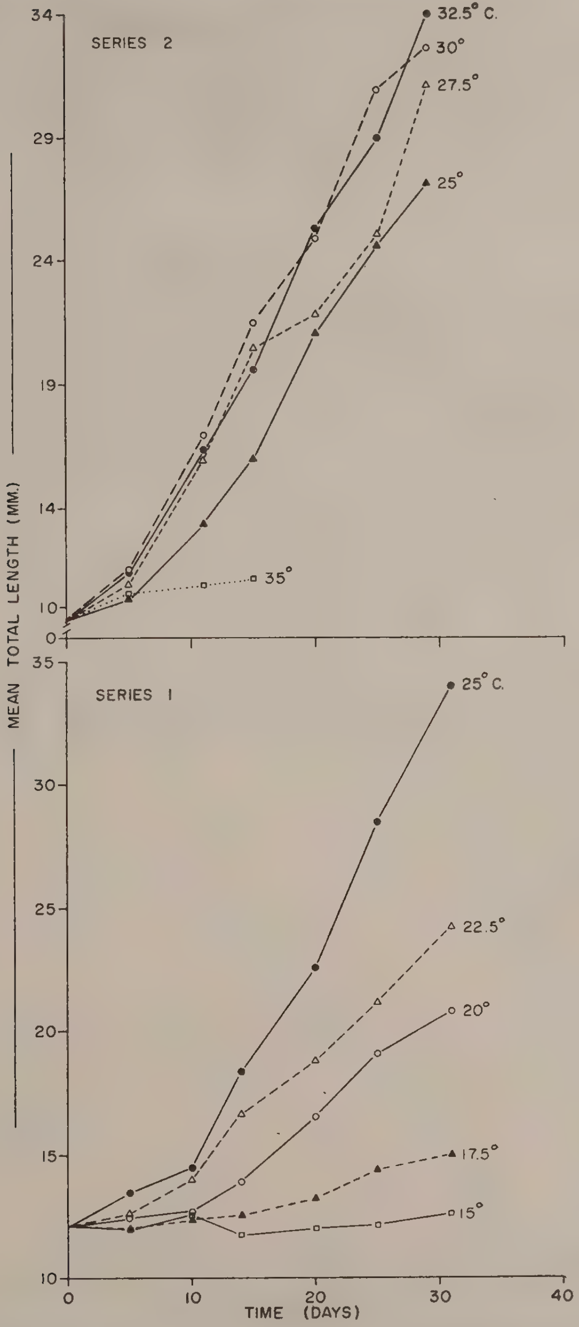

FIGURE 2. Mean increase in length of *P. aztecus* postlarvae exposed to different temperatures for one month.

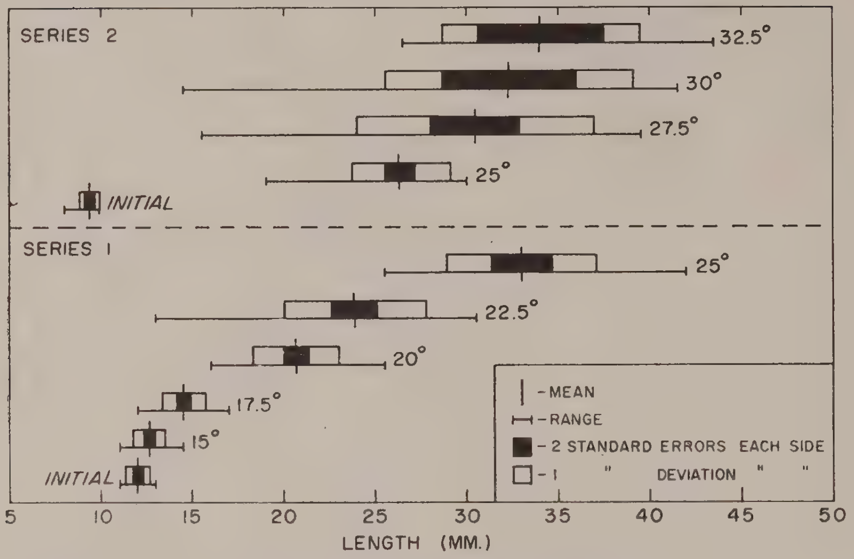

FIGURE 3. Length range (mm.) of postlarval *P. aztecus* surviving exposure to various temperatures for one month.

incubators. The incubators were adjusted over a period of 36 hours from room temperature (approximately 23° C.) to the final experimental temperature.

Experimental animals were fed sufficient live nauplii of brine shrimp (*Artemia*) to keep food constantly available during the month of the study. At each sampling

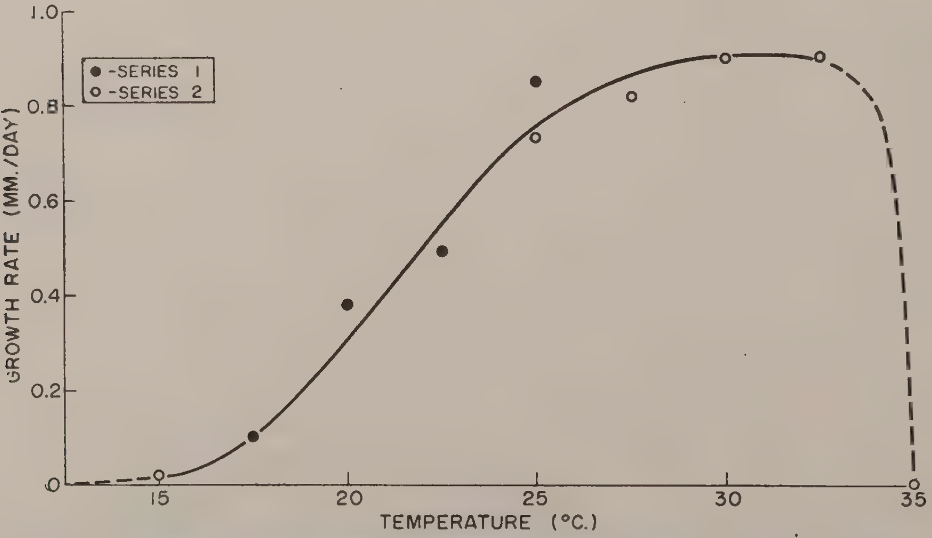

FIGURE 4. Growth rate (mm./day) of *P. aztecus* postlarvae held one month at different temperatures. Rate determined by inspection from straight-line portions of curves in Figure 2.

period (about 5-day intervals), two postlarvae were taken from each aquarium. The 10 animals from a given temperature constituted a sample. Postlarvae were weighed and measured individually as described by Zein-Eldin (1963). At the completion of the study, all remaining shrimp were weighed and measured individually to check the reliability of the sampling procedure (Table I) and to determine the percentage survival at each temperature.

RESULTS

Growth

The final mean size of the postlarvae, whether derived from length or weight (Figs. 1 and 2, and Table I), increased with temperature between 15° and 32.5° C. Growth rate, however, decreased markedly at 35° C., an effect evident in the samples taken on the 11th day. The greatest difference in growth between adjacent temperatures occurred between 17.5° and 20° C. and between 22.5° and 25° C. (Fig. 3). As a result, the increase in growth rate per unit of temperature was greatest in the temperature range 17.5° to 25° C. This differential effect of temperature is illustrated in Figure 4, an S-shaped curve with a maximum (at 30°

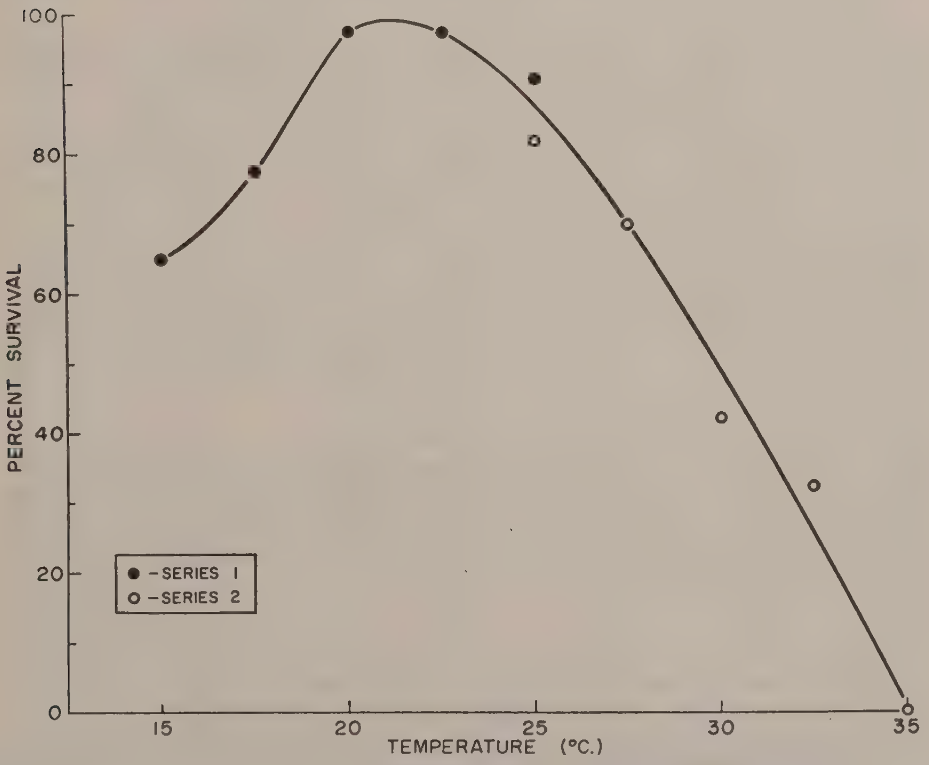

FIGURE 5. Per cent survival of *P. aztecus* postlarvae held at different temperatures for one month.

to 32.5° C.) typical of invertebrate growth responses to temperature (Needham, 1964, p. 416). In Series 2, final size did not differ significantly between groups exposed to temperatures of 27.5° to 32.5° C. (Fig. 3).

Survival

The relation of survival to temperature was somewhat different. The percentage survival increased with temperature between 15° and 20° C., remained above 90% at 22.5° and 25° C., but dropped at temperatures above 25° C. (Fig. 5). At 35° C., no animals remained after the 15th day. A similar decrease in survival at 32° C. as compared with 25° C. was noted in earlier experiments in our laboratory (Table II).

Gross production

Gross production, as estimated by comparing the total weight gains of the postlarvae surviving exposure to each temperature, was used to assess the combined

TABLE II

Comparison of growth of P. aztecus postlarvae from various experiments

Experiment no.	Date	Volume of experimental unit (liters)	No. of animals per experimental unit	Illumination*	Temperature (°C.)	Mean increase in length (mm.)	Duration of experiment (days)	Mean growth rate (mm./day)	Δ^t/Δ^{25}**	Survival (%)
GS-1†	4/62	45	100	+	24.0	19.0	28	0.68	1.00	36
GS-2†	8/62	45	100	+	26.0	17.4	29	0.60	1.00	100
GTS-1††	3–4/63	45	100	+	25.0	22.3	28	0.80	1.00	100
GT-F1	4/64	45	100	+	25.0	25.2	30	0.84	1.00	100
Series 1#	4/64	4	20	—	25.0	21.0	31	0.68	1.00	91
GTS-3	8/64	45	90	+	25.0	20.3	28	0.72	1.00	100
Series 2##	8/64	4	20	—	25.0	17.0	29	0.59	1.00	82
GTS-1††	3–4/63	45	100	+	32.0	32.0	28	1.14	1.38	58
GTS-2	8/63	45	40	+	32.0	30.4	29	1.05	—	34
GTS-3	8/64	45	90	+	32.0	27.2	28	0.97	1.35	100
Series 2##	8/64	4	20	—	32.5	24.6	29	0.85	1.46	32
GTS-1††	3–4/63	45	100	+	18.0	7.4	28	0.26	0.32	100
GTS-2	8/63	45	40	+	18.0	5.2	29	0.18	—	95
GT-F1	4/64	45	100	+	18.0	5.9	30	0.20	0.24	100
Series 1#	4/64	4	20	—	17.5	2.5	31	0.08	0.12	78
GTS-3	8/64	45	90	+	18.0	2.0	28	0.07	0.10	100
GTS-1††	3–4/63	45	100	+	11.0	0.5	28	0.02	0.025	92
GT-F1	4/64	45	100	+	11.0	0.0	30	0.00	0.00	26
GTS-3	8/64	45	90	+	11.0	1.1	28	0.04	0.05	5

* + indicates continuous fluorescent illumination; — continuous darkness.

** Δ^t = mean growth rate at temperature t; Δ^{25} = mean growth rate at 25°.

† Data from Zein-Eldin, 1963.

†† Data from Zein-Eldin and Aldrich, 1965.

# Animals from same population as those in GT-F1.

## Animals from same population as those in GTS-3.

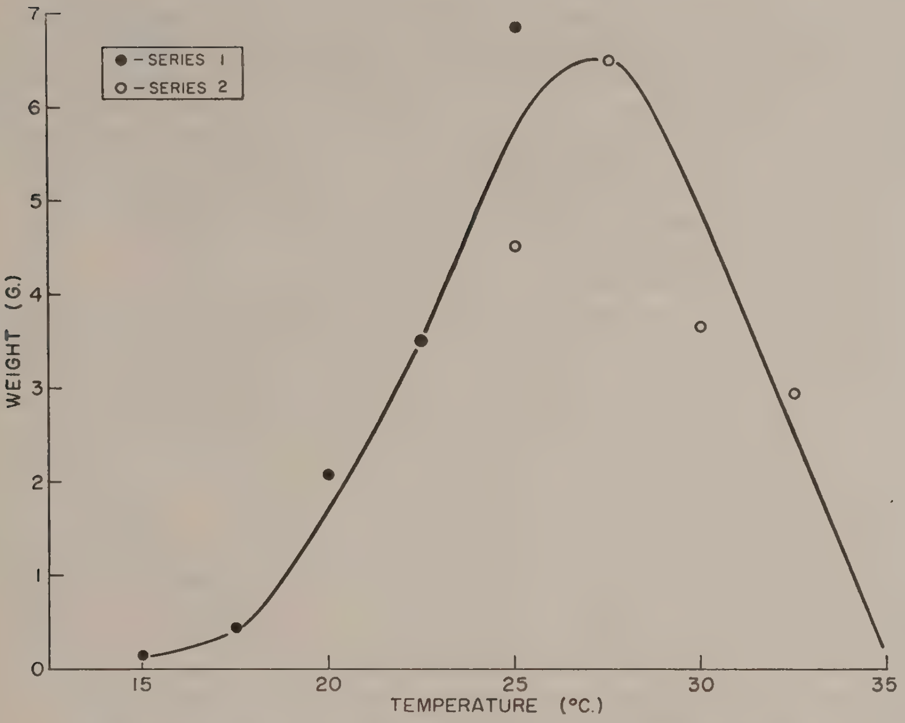

FIGURE 6. Increase in total weight of postlarval *P. aztecus* surviving different temperatures for one month.

effects of growth and mortality (Fig. 6). The total weight gain was maximal at temperatures of 25° and 27.5° C.; under laboratory conditions, the increased mortality at higher temperatures apparently has a greater effect on production than has the accelerated growth of survivors.

Food conversion

The efficiency of food conversion in these experiments was 10% to 15% lower than that determined in previous work in which large tanks and continuous light were used (Zein-Eldin and Aldrich, 1965). Efficiencies were approximately 30% at all temperatures except 15°, 17.5°, and 35° C. The efficiency declined to 15% at 17.5° C. and to 9% at 15° C.

Temperature relations

Growth rates at 25° C. were greater in Series 1 than in Series 2 (Figs. 1 and 2). The previous temperature history of the animals in the two series did not appear to explain the differences in either growth rate or survival. If past temperature history were a major factor in determining growth rate and survival, animals obtained in August would be expected to grow faster and survive better at high temperatures (30° C. and greater) than those obtained in April when temperatures were considerably lower. Conversely, spring animals might be expected to grow and survive somewhat better at temperatures below 20° C. than animals obtained at higher August temperatures. To compare various wild populations exposed to the same conditions, we examined the growth data from several experiments (identified only by code numbers in Table II) performed in our laboratory during the past few years. Spring postlarvae did grow slightly more rapidly at 18° C., but animals collected in August neither grew more rapidly nor survived better at 32° to 32.5° C. than those collected in the spring (Table II).

To obtain further information concerning the effects of temperature on a given population, the mean increase in length of animals held at 25° C. in a given experiment was chosen as a standard, and the growth at other temperatures was compared with that at 25° C. (mean growth at temperature T divided by mean growth at 25° C.; Table II). The ratio of growth to that of the standard was nearly constant at 11° or 32° C., but was variable between 17.5° and 18° C. The variability at 17.5° to 18° C. may arise from the relatively great effect of temperature on the growth rate at this temperature range.

The somewhat reduced growth rates in these series were apparently caused by crowding. Higher growth rates were attained by animals from the same postlarval populations when reared in larger illuminated tanks (Experiments GT-F1 and GTS-3 of Table II). If the growth rates of animals from Experiment GT-F1 are compared with those of Series 1, or rates from GTS-3 with those of Series 2, rates in the two series are 0.8 of those in the larger tanks and, thus, correspondingly larger volumes of water. This reduced growth may have been the result of the smaller water volume per animal (crowding) rather than the lack of light, since subsequent experiments have indicated that effects of light are negligible.

It seems apparent that in laboratory studies, actual growth rates of the animals depend upon the particular natural population of postlarvae used. Comparisons of the relative effects of temperature are, however, valid within a given group of animals.

Ecological Implications

A relation between temperature and growth rate of *P. aztecus* has also been suggested in reports on field studies by St. Amant, Corkum and Broom (1963), and Ringo (1965), who noted an apparent spurt of growth when the water temperature exceeds 20° C. Our results indicate that this pattern is a direct effect of temperature on the growth rate. The laboratory studies reported here also confirm the suggestion of Zein-Eldin and Aldrich (1965) that the influence of temperature on growth of postlarval brown shrimp is most marked in the 18° to 25° C. range.

Within the range of 15° to 20° C., small differences in temperature have a pronounced effect on the time needed for the completion of postlarval development in the laboratory (Fig. 7). The calculated time required for an average laboratory-held postlarva to increase from 12 to 25 mm. decreases from 260 days at 15° to 108 days at 17.5°, and to 36 days at 20° C. Temperatures greater than 20° C. bring about relatively minor decreases in the time required to complete postlarval development. That more rapid growth may occur in nature, where fluctuations

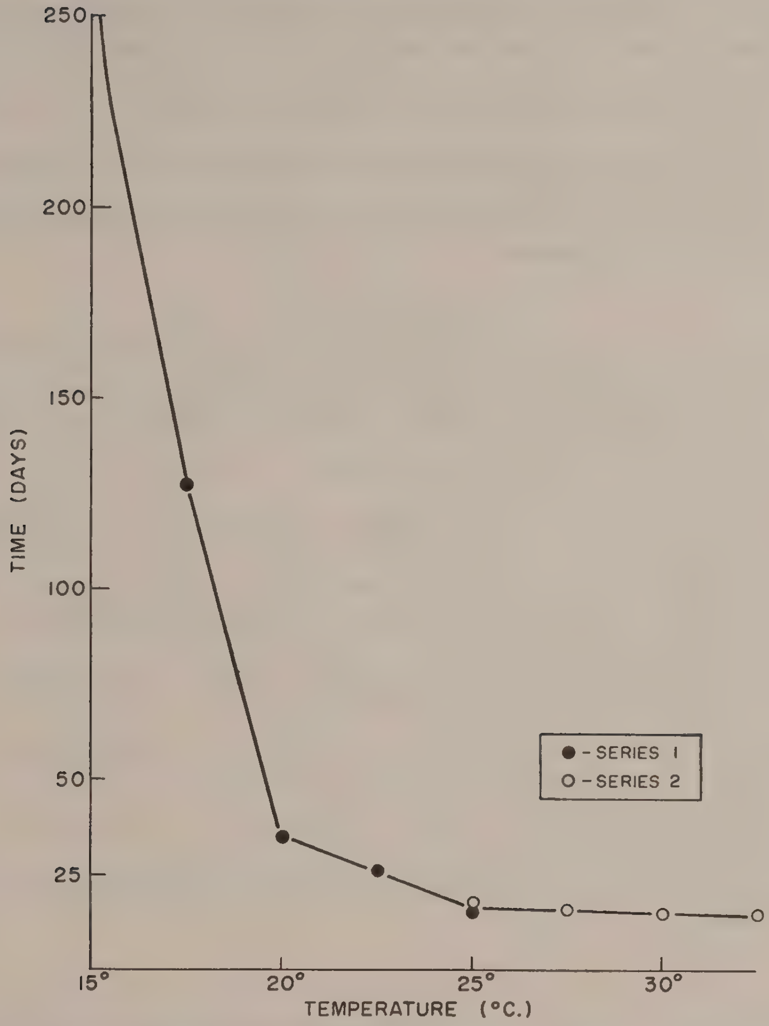

FIGURE 7. Number of days required for a 12-mm. postlarva of *P. aztecus* to grow to 25 mm. at different temperatures (based on slopes in Figure 4).

in temperature are the rule, must be re-emphasized. It is probable, however, that the growth rate below 20° C. is too slow to be readily observable in successive field samples.

Further observations are required to determine the degree to which other natural factors, such as food and light, influence the growth of postlarval *P. aztecus*, as well as that of *P. setiferus*.

SUMMARY

1. The growth of postlarval brown shrimp, *Penaeus aztecus,* was studied in the laboratory at constant temperatures of 15° through 35° C.

2. Growth increased with temperature up to 32.5° C. Maximal increases of growth rate per unit of temperature were observed in the temperature range of 17.5° to 25° C.

3. Survival for one month was markedly decreased at 32.5° C., and no animals survived at 35°.

4. The results suggest that in the laboratory gross production is optimal at temperatures of 22.5° to 30° C.

5. Non-lethal temperatures can have a strong effect on the time required to complete postlarval development.

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